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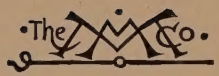
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EXPERIMENTAL ZOÖLOGY

BY

THOMAS HUNT MORGAN

PROFESSOR OF EXPERIMENTAL ZOÖLOGY
COLUMBIA UNIVERSITY

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PREFACE

THE great interest that has been shown during the last fifteen years in the study of Experimental Zoölogy has led to the rapid development of this branch of biology. An attempt is made in the following pages to bring together the results of this work. A series of about thirty-five lectures formed the basis for my treatment of the subject, and this will account, in part, for the way in which the matter has been handled; many details have been omitted that an exhaustive treatment would demand; and the plan has been to select the most typical and most instructive cases for presentation, when such a choice was possible. Nevertheless, I believe that the reader will find a fairly full account of the subjects considered.

Physiology has from the beginning made use of the method of experiment, and with notable success. Morphology has, up to the present time, followed mainly the historical and descriptive methods, although striking exceptions could be cited. While the historical study of zoölogy must always remain a legitimate field for activity, as human history has been a time-honored study, yet there can be little doubt that the more promising and searching method of zoölogical study in the future will be found in experiment.

The central problem of morphology — the causes of the changes in form, or at least the determination of the conditions under which changes in form occur — will furnish the main theme of the present treatise. Two fields of study that properly fall under this head are, however, not considered, viz. experimental embryology and the experimental study of regeneration. Both of these subjects have in recent years received comprehensive treatment in book form, so that it did not seem desirable to go over the ground again. More-

over, their consideration would have demanded too much space to be included with the present matter in a single volume. The fascinating study of the psychical side of living phenomena also belongs to the province of experimental biology, especially comparative psychology; but this subject has quite recently been fully dealt with by Loeb and by Jennings, who have themselves been largely instrumental in developing the subject, so that further treatment would be more than superfluous.

The excellent summaries and reviews of some of the topics discussed here, that have been published in recent years, have greatly facilitated my work. I need only mention Roux's and Driesch's analysis of the experimental method, Gräfin v. Linden's summary of the experiments on butterflies, Herbst's excellent treatment of the subjects of "Formative Reiz," Phillips's very full review and literature on sex determination, and Cuénot's, Lenhossek's, and O. Schultze's treatment of the same subject. I need scarcely add that, while using these and other reviews, I have made my own compilation almost exclusively from the original sources.

Covering as extensive a field as I have attempted to cover, it is probable that the different subjects have received unequal treatment, and I fear that some omissions may have been made. I trust, however, that no serious oversights or mistakes will be found.

It gives me great pleasure to express here my appreciation of the generous assistance in the correction of the manuscript and proof rendered by my wife, by Professor E. B. Wilson, by Professor C. B. Davenport, and by Professor C. E. Castle.

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EXPERIMENTAL STUDY OF EVOLUTION

EXPERIMENTAL ZOÖLOGY

CHAPTER I

THE EXPERIMENTAL METHOD

The study of Zoölogy by experimental methods is not a new departure, for the method of experiment has been often applied to special zoölogical problems. On the other hand, the recognition that only by experimental methods can we hope to place the study of Zoölogy on a footing with the sciences of chemistry and of physics is a comparatively new conception, and one that is by no means as yet admitted by all zoölogists. I do not wish to appear to disparage those studies that deal with the descriptive and with the historical problems of biology. They also offer a wide field for activity, and the more familiar we become with the structure and modes of development of animals, so much the better can we apply the experimental method. In fact, many of the problems of biology only become known to us as the result of direct observation. The wider, therefore, our general information, the greater the opportunity for experimentation.

It is undoubtedly true that many zoölogists who have spent their lives in acquiring a broad knowledge of the facts of their science fail to make use of their information by testing the very problems that their work suggests. This is owing, no doubt, to their exclusive interest in the observational and descriptive sides of biology, but also in part, I think, to the fact that the experimental method has not been sufficiently recognized by zoölogists as the most important tool of research that scientists employ.

Perhaps also the fact that the historical side of biology attracts such popular interest accounts, in part, for the neglect of more searching scientific methods of study.

Whether the method of observation or the method of observation and experiment is followed, seems to be also a question of the kind of interest aroused by living objects. If the number of collectors, naturalists, zoölogists, anatomists, entomologists, ornithologists, mammalogists, conchologists, etc., be compared with the number of physiologists, physiological chemists, bacteriologists, it will be seen that the former have an enormous advantage in numbers. It is true that a few zoölogists are experimentalists, and that some physiologists do not experiment at all, but the proportion remains about the same. In other words, interest in collecting and recording the results of observation and in the artistic side of nature is much more widespread than interest in the study of problems, or, if the interest is not lacking, the will to take the initiative in the formulation and solution of problems seems to be less cultivated in the biological sciences than the power to observe and to describe. In so far as the followers of the one or of the other method of investigation have made their selection as a matter of temperament, the disproportion will probably always remain; but in so far as the result is due to imitation, or to following the line of least resistance, or to a failure to appreciate differences in aim and method, the proportion may to some extent be altered; and I think it will be generally admitted that at the present time there is greater need for experimental work than for descriptive and observational study.

It is sometimes said that experimental study is the analytical study of problems, and this in a sense is true, but it is only a part of the truth. It is rather the method of attacking problems that is the chief characteristic of experimental work, for is not the historical method also a study of problems? We demand in the case of a problem in experimental science that the conditions under which an event takes place be discovered, and that, if possible, we reproduce artificially the result by controlling the

conditions. In fact the control of natural phenomena is the goal of experimental work.

In the studies of physics and chemistry the method of experiment is so familiar, that we think of their advancement as taking place by experiment alone. In biology the situation is different, and new discoveries are looked for as often in the field of observation as of experiment. This difference is due to the higher stage of development that has been reached by the physical sciences, while biology is still, in large part, in the lower stages of its evolution where facts are insufficiently known. Nevertheless the amount of time still given to descriptive work is out of proportion to the present condition of development of biology.

A few examples may serve to illustrate the differences between the descriptive and the experimental study of zoölogy. The egg of an animal, if set free and fertilized, begins at once to develop. Descriptive embryology gives us the different stages through which the egg passes, but no matter how complete the description, we still know little or nothing of the causes that are operating to bring about the development. What, for instance, does the spermatozoön bring into the egg to make it develop? What physical and chemical changes take place during cleavage? What makes the embryo turn in at one pole? Why do certain cells develop cilia? These and a hundred other questions suggest themselves. Observation has failed to answer them.

Another method employed in recent years has been to attempt to find certain physical or chemical changes that seem to be similar to those observed in the developing egg. Thus it has been suggested that the spermatozoön brings a ferment into the egg; that the cleavage is due to differences of surface tension; and that the gastrulation is caused by osmotic pressure. Machines that behave in somewhat similar ways have even been constructed to illustrate some of these changes. Interesting as the ideas derived from these sources may be, their scientific value lies only in their suggestiveness, until it can be shown

that the changes in the embryo are really the outcome of similar processes; and the only way in which certainty can be gained on this point is by experiment on the organisms themselves. If a ferment starts the development it is our duty to isolate it, and to introduce it hypodermically into the egg. If this could be done and the development thereby started *exactly* as in normal fertilization, the hypothesis becomes at least probable that a ferment is brought in by the spermatozoön and starts development. Similarly, for cleavage, for gastrulation, and for every stage in the development, experiment alone can give a satisfactory answer.

The essence of the experimental method consists in requiring that every suggestion (or hypothesis) be put to the test of experiment before it is admitted to a scientific status. From this point of view the value of an hypothesis is to be judged, not by its plausibility, but by whether it meets the test of experiment. Its use is therefore primarily for the investigator, and not for the layman; yet as a matter of fact the wildest speculations are likely to be the ones that excite most popular attention and applause.

It is sometimes said that an hypothesis is useful in proportion to the number of facts it brings under one point of view. This is true for the student rather than for the investigator. Such an hypothesis may have no scientific status. It belongs rather to a system of mnemonics. To the teacher, also, hypotheses are useful in arousing the interest of his hearers, so that by exciting their undeveloped imagination he can make his dry facts more entertaining. But let us be careful to distinguish between the forensic and the scientific value of hypotheses.

Hypotheses may be useful, and have been used in various ways. They have been used, as just stated, to hold together a body of isolated facts; as such they are in reality only fictions. They have been used in the reconstruction of supposed historical events, especially in biology in the setting up of family trees. In this case they can only claim to be more or less plausible suggestions. Hypotheses have been used to direct interest

toward certain fields of study. As such they have often proven stimulating and have been useful in acting as a guide for others. But the hypothesis of real importance is the working hypothesis of the investigator. It is the test by means of which he tries to interpret his problem, and therefore it is essential that his hypothesis is one having a practical bearing, *i.e.* an hypothesis that can be shown to be true or false. It differs in this essential respect from purely fictitious and from metaphysical hypotheses.

The working hypothesis carries along with it its dangers as well as its advantages; since, while it may lead to discoveries, it may, if it is wrong in principle, blind us to the real conditions. Therefore the investigator must not only be an inventor of working hypotheses, but cultivate also a skeptical state of mind toward all hypotheses — especially his own — and be ready to abandon them the moment the evidence points the other way. And herein lies one of the differences between the recorder of observations and the experimenter. The work of the observer, if exact, is complete in itself, and stands forever as a monument to his ability, or at least to his industry; while the conclusions of the experimenter, if they are to bear fruit, must become modified with each new discovery. His results are absorbed in the current of the next advance, but his consolation will be that he has had at least a share in the causal study of living things, and in helping the human race toward the control of organic phenomena.

To return to our examples. The growth of animals and plants offers a wide field for experimental study. Under certain conditions we see a young animal continuing to grow larger until a certain size is reached, when growth slowly ceases. Although the animal may live for many years longer, it has ceased to grow. What makes it grow? Why does it stop growing? We have hardly begun experimental work along these lines; yet we shall see later that there is a promising field for work in this direction. After a time old age comes on and the animal dies. We say it dies a natural death, and this seems inevitable,

but only because we have found that death always takes place under ordinary conditions. Suppose, however, we change the conditions; might we not hope to prolong the duration of life? Improbable as this may seem, there are already experiments afoot that indicate that, however difficult, the problems may not be insoluble.

Why, on an average, in most animals, are equal numbers of two forms born — male and female? Is there an internal mechanism? If so, what regulates it? Do external or internal conditions determine that one egg becomes male, another female? Even if an internal mechanism exists, it might be affected by external conditions, and in any case the cause of the production of the two types must be determined.

Observation has established that the evolution of animals and plants has, in all probability, taken place. But what factors are involved in the process are unknown. Only in the last few years by means of an experimental study of the subject has decided advance been made.

It is sometimes stated that nature has already carried out innumerable and wonderful experiments, and that we can never hope to excel her in this power. Is it not better, therefore, to examine patiently and reverently what she has done, and in this way learn how her processes have been carried out? Let us not be blinded by rhetorical questions of this kind. No doubt nature has carried out prodigious experiments; but we can never be certain that we know how she has obtained her results until we can repeat the process ourselves. What would the chemist or the physicist say if he were told that nature has already carried out experiments on a much greater scale than he can hope to accomplish, and that he should drop his experimental methods and study his physics in a thunderstorm and his chemistry in a volcanic eruption!

I have brought up this point because it illustrates one side of the experimental method that is sometimes overlooked. Almost all of the phenomena with which the biologist has to deal are so complex that he cannot determine what part each factor

plays in the result unless he study the effects of each under different conditions that can be controlled. Little by little, in this way we can hope to gain a clearer insight into the conditions that, taken all together, produce the result.

So much for the experimental method. It is pertinent to ask what is an experiment? If I cut an earthworm in two to see what will happen, have I performed an experiment? Perhaps not, for the actual performance of cutting the worm in two is not the essential point. The essence of an experiment is a trial or test, and the conditions are so arranged that an answer is expected. If the worm is cut in two in order to study the physiological behavior of the two ends, as has been done in fact, with some interesting results, or in order to see what regenerates at the two cut ends, we have a distinct purpose in view, although no formulated problem. If we proceed farther and remove a definite number of segments in order to see how many come back, and then try to determine what conditions are involved in the results, we are clearly carrying out an experiment with a more definite aim. This illustration will serve to show that the most essential feature of an experiment is the anticipation of the results of a test. The operation may be so simple, and the conditions so little known, that to call the performance an experiment may easily expose one to the ridicule of those unfavorably inclined to the claims of experimental work. If the process is carried out with scarcely a thought as to its purpose, and in complete ignorance of all the conditions entering into the problem, it can scarcely be called an experiment at all. At most it is only a preliminary testing of possibilities. Much of the pioneer work in experimental zoölogy has necessarily been of this kind, and crude as such preliminary work must be, it should be looked upon only as the first step toward a further and more critical analysis.

The carrying out of an experiment implies the formulation of a working hypothesis, and this usually presupposes some knowledge of the possible conditions that control the phenomena. The experimental work becomes more explicit and accurate the

more we know beforehand of the possible conditions that may enter into the result. The ability of the experimenter is shown in his insight into the possible factors that may be present. His ability may be the result of a correct estimate of the possible conditions, but for the highest order of work there is demanded also great imaginative power. Good judgment and accurate observation may lead to *fine* work, but constructive imagination seems to be required for the highest order of *original* work. This does not imply that accuracy of observation is not as requisite in original work as in descriptive and observational work, and should always be expected; but the man who sees new and overlooked combinations may open fields of research that will set to work an army of able "investigators."

The branches of biology that have made most extensive use of the experimental method are physiology, bacteriology, and physiological chemistry. The zoölogist and the embryologist have also to deal with physiological problems, and already the beginning of important experimental work has been carried out in this field; but *the most distinctive problem of zoölogical work is the change in form that animals undergo, both in the course of their development from the egg (embryology) and in their development in time (evolution).* It will be granted, I think, that these formative problems are more difficult than those relating to function with which the physiologist has concerned himself in the main; but this is all the greater reason why the experimental method should be used in their study, especially after so much purely descriptive work has been already done.

The term "morphology" has been used in recent times to denote the study of form, as contrasted with physiology, that deals with functional changes. Morphogenesis has also been employed to signify a study of the changes in form through which organisms pass. It is mainly the experimental study of these changes in form that I propose to examine in the following pages. Experimental morphology would perhaps nearly indicate the field to be examined; but since the line between experimental physiology and experimental morphology is often

hard to draw, and since I shall not hesitate at times to enter upon the physiological side of many problems, I have chosen the somewhat broader title of Experimental Zoölogy to include the subjects to be treated.

The principal topics to be discussed fall under the following six headings: —

I. Experimental Study of Evolution.
II. Experimental Study of Growth.
III. Experimental Studies in Grafting.
IV. Experimental Studies of the Influence of the Environment on the Life-cycle.
V. Experimental Study of the Determination of Sex.
VI. Experimental Study of the Secondary Sexual Characters.

CHAPTER II

THE INFLUENCE OF EXTERNAL CONDITIONS IN CAUSING CHANGES IN THE STRUCTURE OF ANIMALS

Animals and plants are so constituted that one of their chief characteristics is that they respond to their natural environment in such a way as to insure their continued existence. These responses are in the main physiological, and therefore in large part transitory; but in some cases the response is structural, involving a temporary or even a permanent change in form or structure that persists at least so long as the external conditions that called it forth remain. The question arises whether these changes, directly induced by the environment, may not give origin to the more fixed characters that have become the permanent inheritance of each species. May not these have been in the first instance adaptive responses to the environment? This leads to the further question of the origin of all the characters of the species, whether adaptive or non-adaptive. In this and in the following chapters the different sides of this question will be considered.

ADAPTIVE RESPONSES

External conditions sometimes cause adaptive structural changes in organisms. We are familiar with some effects of this sort in our own bodies. Pressure on the skin, if long continued, causes it to become thicker and more capable of resisting the injurious effects of pressure. Sunlight tans the skin and protects it from "burning." It is said that cold causes the fur of some mammals to become thicker, and this change better protects them against the cold. Conversely, it is said that horses and dogs lose their hair to some extent in very warm climates.

A number of Arctic animals become white in winter. This change seems to be in part due directly to the cold, for it has been found if these animals are transferred to warmer climates they show less marked changes on the approach of winter.

Flounders and some other fish and some amphibians become lighter in color on a light background and darker on a dark background. The most remarkable case of this sort is that of the pupæ of certain butterflies. If the pupation takes place on a light background, the chrysalids are lighter; and if on a dark background, they are darker. Experiments by Poulton [1] have shown that this effect is produced directly through the skin and not through the ocelli. Poulton thought in one case that even the color of the silk in which the caterpillar incloses itself is influenced by the color of the background, but this has been shown not to be the case.

It is popularly supposed that the African chameleon becomes green in green surroundings, and brown in a dark environment, but this is probably not true; at least it has been shown in another lizard, Anolis, that can also change from green to brown and the reverse, that the animal is as a rule green if warm and brown if cold. The effects are produced by change in the pigment of the dermal pigment cells. In the cold the black pigment spreads out over the surface and conceals the stationary green pigment. In the warmth the black pigment migrating inward exposes the green. Light has a somewhat different effect. In both the African chameleon and in Anolis a strong light acts like a low temperature, causing the black pigment to migrate to the surface, and a faint light or darkness acts like a high temperature, causing the black pigment to wander inward, so that the animal becomes green. Other lizards give reverse effects in light. Parker and Starratt have shown for Anolis that when both light and heat act together, the results are as follows:

[1] For details of the experiment, see Poulton, "The Colours of Animals," p. 110, 1890; "Further Experiment upon the Colour Relation," etc., Trans. Ent. Soc., p. 293, London, 1893; "An Inquiry into the Cause and Extent of a Special Colour Relation," Proc. Roy. Soc., Vol. XII, 1887.

At a low temperature, 10° C., Anolis changes from green to brown, irrespective of illumination. At a high temperature, 40° to 45° C., it turns from brown to green, irrespective of illumination. Thus heat is the controlling factor at these extremes. Between these extreme temperatures there is a range from 25° to 35° through which light is the controlling factor, although heat is not without its influence, as shown by the rate of the change. Parker and Starratt have discovered the astounding fact that the effects of the illumination may be produced when an area of the skin no larger than a square millimeter is exposed, the rest of the animal being in the dark.

The changes that have just been described, except perhaps the last ones, seem to be of benefit to the animal, either in directly protecting it from the agent that brings about the result, as in the effects of pressure, cold, sunlight, etc., or in more effectually concealing the animal from its enemies. These responses are said to be adaptive, but it is remarkable how rare are adaptive *structural* responses, when we recall the fact that adaptation of the organism to its surroundings is one of its most characteristic properties. The poverty of adaptive structural response does not encourage one to look to external agents as having brought about directly the structural adaptation of organisms to external conditions, even if it could be shown that such influences are inherited.

There are, on the other hand, many cases of physiological responses that are adaptive; in fact, nearly all functional changes are directly beneficial to the organism. Animals respond in a most remarkable way to poisons. If certain alkaloids are injected in ever increasing doses, the animal becomes immune to a dose which if given in the first instance would have been fatal. In the case of the poisonous ptomaines produced by bacteria, the animal produces a counter poison, an antitoxin, that nullifies the effects of the ptomaine. In a number of bacterial diseases the animal becomes more or less immune after the first attack.

Equally striking are the adaptive responses shown by animals

to temperatures higher or lower than those to which they are normally subjected. If the change of temperature is gradual, the organism may become adapted to a temperature that would have been fatal if met at once.

Somewhat similar results have been found by subjecting marine animals to water containing less salt. If the change is gradual, the animal will become adapted to the new density. The extent to which the process may be carried differs greatly in different species. In some cases the animal may be gradually transferred even to fresh water. There are also other animals that may pass at once from salt to fresh water without serious injury. Salmon and shad leave the ocean to migrate up the rivers, and other fish do the same thing. Conversely, the young salmon migrates back to the sea. The number of fish that will stand as great a change as this is, however, limited, although many oceanic species will live in water much less salt than that of the sea.

NON-ADAPTIVE RESPONSES

In contrast to the few cases of adaptive structural responses to the environment there are quite a number of cases in which definite structural responses occur that are not adaptive. One of the interesting points connected with these responses is that the differences effected by changes in the environment have been shown in some cases to resemble the kind of differences that separate species from each other; but whether species have really originated, either directly or indirectly, in this way, must be carefully considered later.

Influence of Temperature on the Coloration of Butterflies

The earliest experimenters on the influence of temperature on butterflies were Dorfmeister (1864) and Weismann (1875). Earlier naturalists, who were familiar with seasonal dimorphism in butterflies, had supposed, it is true, that differences in temperature might be responsible for the differences in color that characterize the summer and the winter broods; but it

required the experimental work of Dorfmeister and of Weismann to show that this supposition was correct.

Weismann showed for Vanessa levana-prorsa that when a pupa, destined to give rise to the summer form, is kept at a low temperature, it may produce the winter form, V. levana, or a type transitional between the summer and the winter forms. He also succeeded, by raising the temperature, in changing the winter pupa so that it gave rise to the summer type of butterfly.

More recently Merrifield, Standfuss, Fischer, Gräfin von Linden, and others have carried out extensive experiments on the effects of temperature. The butterflies and moths used for this work are usually those having summer and winter broods, that differ in color and often in size, and even in the shape of the wings. In other cases, however, similar changes have been brought about in forms that do not show seasonal dimorphism. It has been found that not only the summer form can be changed into the winter form, and *vice versa*, but in certain cases the type may be changed by cold so that it resembles northern varieties of the same species, and by heat to resemble southern varieties. Temperatures that are only somewhat higher or lower than normal produce the southern and northern types respectively, while much higher or lower temperatures produce effects that are rarely or never found in nature. These latter changes are sometimes called aberrations. We may first examine a few examples of these effects given by Standfuss.

The effect of heat on Vanessa cardui is shown in Fig. 5. The colors are much lighter above than those of the normal butterfly. The black bands are much reduced. Similar changes are observable on the under side of the wing. The pupa had been kept for 60 hours at 36–37° C., and then at normal temperatures for six to seven days, when the butterfly emerged. The effect of cold on Vanessa cardui is shown in Fig. 6. The color is darker and the white spots are reddish in tint as seen especially on the under side. The pupæ had been kept for 33 days in an ice chest, then for five days in a cellar (+13° C.), and lastly for nine days at room temperature.

FIG. 1. Showing the influence of heat and cold on the pupæ of some butterflies. Vanessa antiopa: Fig. 1, effect of heat; of cold, Figs. 2 and 3. Vanessa cardui: Fig. 5, effect of heat; Fig. 6, effect of cold. Vanessa atalanta: Fig. 7, effect of heat; Fig. 8, effect of cold. Fig. 4, Vanessa pollychloros, aberratio dixeyi, effect of cold. (After Standfuss.)

The effect of heat on Vanessa atalanta is shown in Fig. 7. The blue spots on the outer edge of the wings are so much reduced that often two small flecks alone remain. The red cross-band of the fore-wings is spread out. In the black, that is somewhat brownish, red-brown shading appears near the base of the wing. The large white spot at the anterior border of the fore-wing and the neighboring five scattered white spots show a reduction, and the latter may even disappear. In all of these aspects the type approaches a variety from the Canary Islands. The pupæ were kept 172 hours at 37° C., then three to four days at 24° C.

The effect of cold on Vanessa atalanta is shown in Fig. 8. The ground color of the upper surface is bluish black. The white spots are larger, and the whole of the outer tip of the fore-wing is lighter. The red cross-band is reduced and broken. The under surface of both wings are much changed, as the figures show.

The influence of heat and of cold on Vanessa antiopa is shown in Figs. 1 and 2. The effect of heat (Fig. 1) is to make "dusty" the brown ground color of the upper surface, especially on the hind wing, that may become nearly black. The blue spots of the marginal row are reduced to half their normal size and are more violet in color. The characteristic yellow margin is dusted with brown. The pupæ had been kept 60 hours at 37° C., and then for 12 days at 24° C. The influence of cold is shown in Fig. 2. The blue spots are much larger, and the ground color of the wings is darkened. The marginal yellow band is reduced and richly dusted with black scales. The pupæ had been kept for 44 days in an ice chest, and then for 15 to 19 days at normal temperatures. Another individual produced by cold (29 to 34 days) is shown in Fig. 3. It approaches Vanessa polychloros, Fig. 4, in a number of points.

Fischer has obtained some very aberrant forms of Vanessa antiopa by heat and by cold. Some of those produced by cold are shown in Figs. 1–8 as seen from above, and in Figs. 9–11 as seen from below. The former set (Figs. 1–8) is arranged to

show how the broadening of the yellow margin begins in the posterior wings and finally extends forward to the same extent on the anterior wings. The change is in an antero-posterior direction. The conditions under which these butterflies had been kept were as follows:—

In the first experiment 20 pupæ of Vanessa antiopa, about 12 hours old, were kept for six hours at a temperature of 14° C. and then four hours in a temperature decreasing from 14° C. to 0° C. After this they were put three times daily for a short period in a temperature of −3° for 18 days. They were then kept in the cellar (14° C.) and finally at room temperature (22° C.). Six pupæ died, the remaining 14 began to emerge after 10 to 12 days. Figure 7 shows one of these butterflies which is the aberration known as hygiæa; another is shown in Fig. 6, in which the blue spots and the dark border have completely disappeared, but the yellow border does not extend inward so far as in the last case. Three other individuals (Figs. 2, 3, 4, 5) show transitional forms in some of which traces of the blue spots could be seen. The last butterfly of this series to emerge was like the normal antiopa with the blue spots even larger than the normal, but less sharply defined. Thus under identical external conditions quite a range of colors result; but of course the caterpillars themselves had probably not lived under identical conditions, nor had they been subjected to the cold at precisely the same stage in their pupation.

In a second experiment the conditions were the same, except that the pupæ were brought into the extreme cold (three times daily) for only 14 days. Five of these showed the aberration *artermis* (like that in Fig. 1, which developed, however, under different conditions).[1] The five individuals showed also aberrations with the hygiæa characters. Two individuals were like Fig. 4; the others were like the intermediate forms.

In a third experiment the conditions were the same as before, except that the pupæ were brought into the extreme cold for only six days. They produced one normal butterfly; one transi-

[1] The butterfly had been kept at a temperature below 0° and 6° C.

FIG. 2. Vanessa antiopa: Figs. 1–8 showing effects of a low temperature on pupa. (After Fischer.)

tional form like Fig. 3; one form, the aberration *artermis*, with many groups of golden scales on the brown ground color and the black border, and even within the blue spots; the rest for the most part belonged to the aberration hygiæa, one of these being as extreme a form as that shown in Fig. 8.

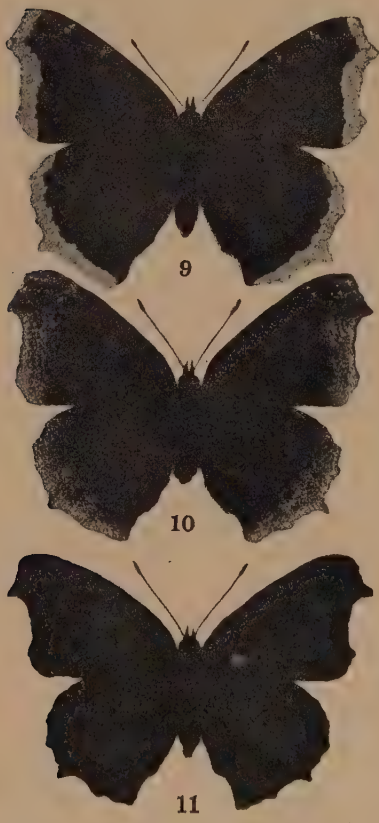

FIG. 3. Vanessa antiopa, under surface: Figs. 9–11 showing influence of cold. (After Fischer.)

The under side of the wings of these butterflies is also changed, but not always in the same way as the upper side. As shown in Fig. 10, not only does the yellow border of the wing extend inward, as it does also on the upper side, but at the same time the black scales spread toward the periphery, darkening the broader yellow band, as shown in Fig. 10. This figure shows the under side of the aberration hygiæa. In the butterfly shown in Fig. 11 the whole under side is black, the yellow border having disappeared. This is the under side of the butterfly shown in Fig. 8 that had the broadest development of the yellow band on the upper side.

Some further details may now be considered. Merrifield did not employ very extreme temperatures. The pupæ were either iced (33° F.) or only cooled (39° to 57° F.). For "forcing," temperatures not higher than 70° to 80° F., or even 90° F., were employed. He found

in general that cooled or iced pupæ gave dark and much-spotted moths, while "forced" pupæ were pale and spotless or with reduced spots. He states that the *markings* are affected by long-continued exposure, especially during the early pupal period, but the *color* is chiefly affected during the penultimate period.

Standfuss has experimented on as many as 7000 individuals in all. He determined that the period in the life of the pupa when it is most sensitive to heat is at the beginning, although it is best not to try to produce the effect too soon after the caterpillar has become a pupa. If exposed soon to extreme cold, the pupæ die; but if exposed soon to heat the best results, *i.e.* the most divergent forms, are obtained, although the mortality is high. If the pupa is exposed as soon as it can stand it to extreme cold and then to heat, the heat-type is produced. In other words, the cold delays the development so that the heat produces the greater effect; for as soon as the temperature is raised the development goes forward rapidly. To get the best effect from cold, Standfuss found it advantageous to expose first to low temperatures, then for 5 to 10 days to moderate cold (11° to 14° C.), and lastly bring the pupæ to room temperature.

In his earlier work Fischer subjected the pupæ for several days to extreme temperatures of heat or of cold, but later he found it better to subject the pupæ two or three times a day to the extreme temperatures during a period of 11 to 20 days. This method applies particularly to extreme temperatures. For a low temperature he used 0° C. or −3° C. or even −8° to −20° C. The high temperature was from 35° to 46° C. The more extreme the temperature that the pupæ will stand the greater the effect produced. Thus temperatures between 0° and −20° gave greater effects than those between 0° and +10°. Temperatures of 42° to 46° gave more striking results than those of 35° to 41° C.

The most important result obtained by Fischer was to show that the same aberrations are obtained by extreme heat and by extreme cold. The result may seem puzzling, but it must be remembered that the coagulation of proteids, which is probably

one of the factors in the results, can be caused artificially either by a high or by a low temperature. In a mixture of proteids we might expect some slight differences in the results of coagulation, even if the principal changes are the same, and it is not improbable that such minor differences do exist.

An excellent general review of the effects on the colors has recently been given by Gräfin Marie von Linden. She points out that in the Vanessa series, a higher temperature makes the red or yellow deeper or more fiery. The dark background suffers a reduction. Cold gives the reverse, a brightening of the general dark ground color, the yellow expanding at the cost of the red. There is also a lightening of the red and increase of white scales. Extreme heat and cold, as stated above, give remarkably similar results. The black spots on the border run together, so that the peripheral dark spots are lost. The dark border zone becomes clearer (in some forms only at the tip). Despite this peripheral clearing up, extreme temperatures cause an increase of dark pigment elsewhere. It may be said, therefore, that extremes of heat and of cold do not give specific effects, but produce the same physiological change.

As a result of these changes the differences between related species sometimes seem to disappear to a greater or less extent. The nearer the forms experimented upon, the more alike are their aberrations. This result led Fischer to the conclusion that extreme heat and cold cause an *atavistic* return to the primitive type of all the Vanessas, *i.e.* a return to the stem-form from which they have come. He attempts to explain this result on the grounds that during the development of the color the butterfly passes in its ontogeny through phylogenetic stages. Cold and heat cause an arrest of development, so that an ancestral stage emerges.

Standfuss, on the other hand, looks upon the changes as something new, and points out certain contradictions to Fischer's idea that the aberrations are atavistic. For instance, the males are much less prone to atavism than the females, and yet produce a much greater number of aberrations. He thinks it im-

probable that the original form of the Vanessas was darker than the present forms, to judge by related groups. Uncertain as arguments, *pro* and *con*, based on these phylogenetic speculations necessarily are, there is fortunately experimental evidence that shows how little ground there is for Fischer's argument. Gräfin Marie von Linden has examined the developing pigment in the wing itself. She finds that the lighter colors develop first and that in the younger stages the red and yellow tones occupy a greater area than they do later. This is the reverse of Fischer's primary assumption of sequence. In pupæ exposed to freezing and to heat it seems that disturbances in the development of the color occur. Standfuss observed in these circumstances that the color develops later than in the normal; and von Linden finds that the black color appears relatively earlier than the others, and at times even before the red and yellow.

Gräfin von Linden has also shown that changes in certain colors similar to these shown by the pupæ can be produced *in vitro*. Extracts of the red color, when heated, become fiery red or more red-brown in color; while on ice the red and the yellow-red tone remain constant. It is likely, therefore, that some of the effects of high and low temperature can be explained entirely as due to the direct influence of the temperature on the chemical composition of the pigment.

Not only have the summer and winter forms been changed by changing the temperature, but in two cases, in which sexual dimorphism exists, it has been possible to change the female coloration into that of the male. For example, the colors of the female of Parnassius apollo can be changed into those of the male. In the female of Rhodocera rhammi the white coloration of the wings can be changed by warmth into the intensely yellow color of the male. It has been suggested that while ordinary temperatures suffice to cause the development of the deeper color in the male, it requires a higher temperature than that ordinarily met with to cause the same change in the tissues of the female. Standfuss has pointed out that while in many cases a lower temperature may cause a darker color and a higher

temperature a lighter one, this is not invariably the rule, as seen in certain dimorphic forms. Thus, in Lythria rotaria the butterfly that hatches in the spring (from over-wintering pupæ) is darker than the summer type (the second generation, variety L. purpuraria). On the other hand, Vanessa levana (also from over-wintering pupæ) is *lighter* than the summer variety, V. prorsa. A lower temperature does not therefore always produce darker colors and a higher temperature lighter ones, although this is the general rule, but the reaction depends also on the nature of the organism.

In these experiments with butterflies the more conspicuous result is the change in color; but it should not be forgotten that changes in size also often occur, and even constant changes in the shape of the wings have been observed, the outline of the wing in some cases being quite different from that of the normal animal.

Effect of Temperature on Caterpillars

Standfuss has shown that by rearing caterpillars at a higher temperature (20°–25° C.) than normal, the characters of the moths may be affected.[1] Changes in the shape of the wings are sometimes caused in this way. The color is also altered to some extent. The most constant change, however, is in the size. Standfuss gives the following rule: "The more the feeding period of the caterpillar is shortened by raising the temperature the smaller the butterflies. Lasiocampa quercifolia, for example, had its weight decreased in this way to one seventh of the normal. On the other hand, if the time of feeding (or in other words the time of the caterpillar stage) is not, or only very slightly, shortened, despite the higher temperature, there is an increase in size, which in the case of Arctia fasceata may be as much as half again the entire normal weight."

Standfuss points out that results similar to these are found in nature where the size of certain forms appears to be connected with the time of year at which the pupæ appear. Species

[1] Merrifield also has made observation on the effects of temperature on caterpillars.

whose growth occurs in late autumn (with lower temperature and decreasing vegetation) and is completed in the autumn so that they winter as pupæ, are generally smaller in the first generation and larger in the second or summer generation; for the caterpillars of the latter are born in summer and have plenty to eat. Conversely, species which winter over as small caterpillars and develop further during the favorable conditions of spring produce larger butterflies in the first than in the second generation.

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CHAPTER III

THE INFLUENCE OF EXTERNAL CONDITIONS IN CAUSING CHANGES IN THE STRUCTURE OF ANIMALS (*Continued*)

Experiments on the Influence of the Food Plant

PICTET has studied the influence of the food of the caterpillar on the color, the size, and other characters of the butterfly. As a rule the caterpillars of each species are found on a particular plant, and cannot be induced to eat the leaves of a different one, or only with great difficulty. A few species, however, are polyphagous, *i.e.* they feed on a number of different plants. For example, the caterpillars of the Arctiidæ feed upon all sorts of herbaceous plants; many Noctuidæ consume indifferently several species of Compositæ; Papilio macchaon lives on different Umbelliferæ; Ocneria dispar, Porthesia chrysorrhæa, and Bombyx neustria are found on nearly all kinds of trees.[1] Occasionally caterpillars are found on plants that are not those normal for them, and the question has often been asked whether the aberrant types of butterflies sometimes met with may not have arisen in consequence of a change in the food plant. This question Pictet has studied experimentally.

In captivity certain caterpillars adapt themselves readily to very different kinds of food. As a rule a caterpillar will feed on the flowers of its natural plant, and even the fruit may be used, as in the case of Cossus cossus, which will eat pieces of apple instead of the wood and the bark of the tree.

It appears that in nature, also, certain species have recently extended their dietary. Thus Lasiocampa quercus was known at the time of Linnæus to feed on the oak tree (as its

[1] These examples are given by Pictet.

name implies) and on the leaves of certain shrubs. It is now found on a number of other trees.

Certain aberrations have been traced directly to the food of the caterpillar. The caterpillars of Ellopia prosapiaria living on the pine become reddish butterflies; but if they occur on the fir, they give rise to the aberration prasinaria, which is green. An analogous case is that of Cidaria variata, whose caterpillars living on the fir give rise to a form that is gray, but on the pine produce a variety obeliscata, which is brownish red.

In certain countries where a variety almost entirely replaces the parent species it is not uncommon to find the caterpillar on a different plant. For example, Lasiocampa quercus lives on different food plants in different countries. In Scotland, where the variety callunæ dominates, the caterpillars live on the heather; in the South, where the variety roboris is found, the caterpillars live on the oak, Quercus robur.

In changing the food, Pictet often made use of plants that were very different from the natural one. Thus the oak was often replaced by the esparcette,[1] by the dandelion, by the lettuce or by the pimprenelle.[2] In other cases it was replaced by the walnut, neflier,[3] and the sorbier.[4] In some cases a food plant closely related to the normal was the only one that could be substituted; thus the European Evonymus europæus (spindle tree) can be replaced by E. japonicus. Certain species refuse all food but their natural one. Other species can be induced to take a different nourishment, but only after much perseverance. Others, such as Lasiocampa quercus, when young accommodate themselves to nearly all kinds of vegetation, but once full size, many plants are rejected. The acceptation of a new kind of food is transmitted by heredity, and individuals whose parents have become accustomed to a strange food will consume the same food with greater facility. Some of the effects that Pictet obtained by changes in the food are as follows: —

[1] Onobrychis sativa, or holy clover.
[2] Poterium sanguisorba, or salad burnet.
[3] Mespilus germanica, or mespit.
[4] Sorbus ancuparia.

The typical male and female moth of Ocneria dispar are shown in Fig. 1 and Fig. 2. In the male the wings are *gray*, *ash*, or *dusky*, with four zigzag black lines. The female is whitish gray or slightly yellow, with the same grayish white

FIG. 4. Ocneria dispar: male, Fig. 1; and female, Fig. 2. First generation fed on walnut leaves: male, Fig. 3; female, Fig. 4. Second generation fed on walnut: male, Fig. 5; female, Fig. 6. First generation on walnut, second on oak: male, Fig. 7; female, Fig. 8. First generation on walnut, second on oak, third on walnut, fourth on walnut: male, Fig. 9. (After Pictet.)

pattern as the male, but more marked. The normal food is oak or birch. The young caterpillars can be made to eat the leaves of the walnut (Juglans regia), at first with difficulty, but the subsequent generations eat it with avidity. The male of the first generation is shown in Fig. 3. The wings are pale yellow, the

central lines have partly disappeared, and the rest of the pattern is less marked. The female of this first generation is shown in Fig. 4. The wings are slightly transparent, with rarely a darker mark on the upper surface. The insect is almost white.

The caterpillars of the next generation were also fed on the walnut. The male is shown in Fig. 5. The wings are whitish, the marginal band has partly disappeared, and the transverse lines are but slightly visible. The female is shown in Fig. 6. The wings are transparent; the V and the fifth of the marginal points alone remain of the markings.

The figures show a decided decrease in the size of the individual, which is accompanied with a constitutional weakness. It was not possible to obtain eggs from this generation. Pictet resorted, therefore, to the device of feeding the first generation on the walnut, the second on the oak, and then the third and even the fourth on the walnut. When the first generation was fed on the walnut and the second on the oak, the male moth appeared as in Fig. 7, and the female as in Fig. 8. The figures show that the effects, produced by feeding the first generation on the walnut, persist during the second generation when returned to the normal food.

In another experiment the caterpillars were fed first on walnut, then on oak, and then on walnut. The male was much like that produced by two generations of walnut, as were the females also. Another lot was fed walnut (1st gen.), oak (2d gen.), walnut (3d gen.), walnut (4th gen.). The male type is shown in Fig. 9. The wings are gray ash, or dusky; the marginal points strongly marked, as well as most of the transverse lines. The marginal band is accentuated in the four wings. The females have white wings — sometimes yellowish. As in the male, the lines and the marginal band of the lower wings is much accentuated. Thus while the greatest change is effected by walnut, oak, walnut, there is a return to the darker type if walnut is used again for the fourth generation. Pictet interprets this as a return to the ancestral type; the result of becoming accustomed to the walnut, and states that he has ob-

tained similar results in other experiments. It is not entirely clear from his figure that the darker form in the fourth generation is really a return to the ancestral type — at least the possibility of a different interpretation must be kept open.

Another experiment showed that when the first generation was fed on walnut, and the second and the third on oak, the effects of the walnut were still apparent in the last generations.

When the first generation was fed on walnut, the second on the oak, and the third on flowers of different kinds (rose and peony), the last seemed to accentuate the effects of the walnut and "tend to cause to disappear those of the normal food. To the same extent as the walnut the flowers appear to be a poor alimentation." The caterpillars of Ocneria were also fed on other plants, the results being in some respects like the preceding cases, in others different.

There are two known aberrant forms of the moth Psilura monacha. The typical male form is shown in Fig. 10, and the female in Fig. 11. The aberrant form *nigra*, male and female, is shown in Figs. 12 and 13, and the form *eremita*, male and female, in Figs. 14 and 15. The caterpillars are found on oak, birch, and conifers.

Caterpillars fed on oak and on birch produced moths of all three types, in the proportion of 58 per cent type-form; 24 per cent ab. *nigra*, and 18 per cent ab. *eremita;* fed on walnut the proportions were 38 per cent type-form; 23 per cent ab. *nigra;* 30 per cent ab. *eremita*. The moths were smaller than the average. The proportion of the aberrant forms is greater from the walnut than from the normal food. In the second generation, nourished on the walnut, the females of the type form assume the characters of the typical males.

In all, Pictet's experiments with feeding included 21 species, comprising 4695 individuals. In nearly all cases some effects of a change from the normal type could be directly traced to the food.[1]

[1] For somewhat similar experiments see Romanes, "Darwin and After Darwin," II, pp. 217–218.

Pictet has also tried the effects of insufficient nourishment, using smaller amounts of the normal food. In the case of Pieris cratægi, lack of food during the last days of the life of the caterpillar causes the wings to become lighter in color and more transparent. If all food is removed from the full-grown

FIG. 5. Psiluria monacha: typical male, Fig. 10; and female, Fig. 11. Aberrant form P. ingra: male, Fig. 12; female, Fig. 13. Aberrant form P. eremita: male, Fig. 14; female, Fig. 15. (After Pictet.)

caterpillar of Vanessa urticæ, it becomes a chrysalid in a few days after the last moult. The butterflies are dwarfs, but show no changes in coloration. On the other hand, if the very young caterpillars are kept on a régime that becomes less sufficient every day, they become pupæ even before the last moult, and produce dwarf butterflies that have the aberrant characters much accentuated.

It is not difficult to starve caterpillars, but it is difficult to make them take more food than they do normally; yet by indirect means this can be done by giving them food containing an excessive amount of nutritive substances.

Reviewing the results of the effects produced by changes in food, Pictet points out that, in general, the variations produced are either in the direction of lighter (albinistic) or darker (melanistic) shades. If the kinds of food that produce the former effect are compared with those that produce the latter effect, it will be seen that the lighter colors result from feeding on plants which, owing to their anatomical structure, present obstacles to mastication — either as a result of a thick epidermis or of the presence of crystals or of hairs, etc. In consequence of the imperfect nutrition of the caterpillar, the butterfly is less pigmented. On the other hand, the melanistic or black variations result from those plants that offer no obstacles to mastication or nutrition. The caterpillars develop rapidly, acquire a size greater than the normal, and the butterfly shows a greater development of pigment.

The influence of different food plants in causing an albinistic or melanistic change in the moths can be traced, according to Pictet, to the length of the pupal stage, and this in turn to that of the caterpillar stage, which again is due to the amount of nourishment received. Thus, those food plants that give insufficient nourishment prolong the caterpillar stage; but this leads to a shortening of the pupal stage, and the albinistic effect is produced, because the dark pigments do not have time to develop extensively. Conversely, an abundant nourishment shortens the caterpillar stage; but this causes a prolongation of the pupal stage during which the pigments have time to develop even more fully than normally, and the melanistic variation is the result.

Not only the colors of the moth or butterfly are affected by the character of the food, but the colors of the caterpillars themselves may sometimes be affected, although to a less degree. Pictet finds, in fact, that there is a correlation between the pig-

mentation of the caterpillar and of the adult. The caterpillar of the death's head moth (Acherontia atropos) is ordinarily yellow, but has also a black type. Dasychira pudibanda is white, but has a green and gray variety, etc.

The color of many caterpillars is much influenced by the food in the digestive tract that can be seen through the semi-transparent skin. Poulton has also shown that certain of the epidermal pigments are derived from the chlorophyll absorbed with the food. He separated into three groups caterpillars of Agrotis pronuba: the first was fed with the green leaves of cabbage, the second with the yellow etiolated leaves. Both lots developed their normal yellow-brown color. A third group was fed on leaves deprived of the green and of the yellow coloring matter, and only the brown pigments developed. Standfuss has produced within a few hours color changes in the caterpillar of Eupithecia absinthiata. It becomes "a lemon-yellow when fed on the yellow bunches of Solidago, green on non-flowering leaves of the same plant, rose on the 'buttons' of Statice armeria, white on the umbels of Pimpinella saxifraga, brown on the bouquets of Artemisia vulgaris, and a delicate blue on the small balls of Succisa pratensis." Similar results are known for other forms. Pictet finds also that the colors in certain caterpillars that hibernate tend to disappear, but reappear again a few days after feeding begins again in the spring. The colors of some species change with each moult. Difference in the color, and even in the markings of caterpillars, occur when they are fed on food other than the normal. In some cases the effect is direct, as explained above; in other cases the effects are indirect, *i.e.* not due to the food in the digestive tract or to the pigments directly absorbed and present in the skin or in the blood. In the case of Ocneria dispar the food plants that produce lighter colors in the moths have the same effects on the caterpillar. Similarly for the dark or melanistic changes. Moreover, the effects may last over for one or two generations after the caterpillar is again fed on its normal food.

The Influence of Light, Electricity, Centrifugal Force, Chemical Substances, and Oxygen on the Caterpillars and Pupæ of Moths and Butterflies

It has been shown by Gräfin von Linden that the size, the colors, and the markings of butterflies may be altered by subjecting the caterpillars or the pupæ to several kinds of external conditions other than temperature. In general, however, the results are similar to the effects produced by higher and lower temperatures.

Light. — Vanessa urticæ and V. io were used. Some of the caterpillars were kept, with their food, in red, or green, or blue light. Others were kept in the dark. The principal changes were in the ground color of the wings of the butterflies. This was intensest and brightest in red light, dusky in green, and paler in blue and in the dark. The butterflies of V. urticæ were largest from the caterpillars reared in the blue, and of V. io in the dark. The changes in the markings were very slight.

Electric Shocks. — The pupæ of V. urticæ, in a fresh but dry condition, were put into an iron box through which an electric current was passed of sufficient strength to cause a pricking sensation when applied to the hand. In other cases one electrode was applied at the wing axis and the other at the tip of the wing case. The resulting butterflies were brightly colored. The black border of the wing was broader, and the tip of the wing was sometimes dark. The blue and yellow scales of the sides of the wing were little developed.

Centrifuge. — After the pupæ had become hard they were subjected to a centrifugal force for ten minutes each day. The effects were in general similar to those caused by light.

Chemical Substances. — Contrary to the results of Standfuss, who found changes in the food had no influence on the color of the moth, except in one case, when salt was added to the food of Callema, Gräfin von Linden found that certain substances given with the food produced distinct effects. Some effects, for the most part slight, were obtained with (1) defibrinated blood;

(2) iron albuminate (officinal solution: 4 parts metallic iron to 1000 water); (3) argonin silver casein (5 per cent); (4) sugar; (5) lupulin; (6) capsicum; (7) morphine (1 per cent); (8) atropin (1 per cent).

The iron and the silver compounds by exciting hunger tended to produce larger forms. The largest butterflies came from caterpillars fed with argonin silver casein and the smallest from those given morphine with their food. The younger the caterpillars, when the experiment began, the better the results. Darkening of the *ground color* of the wings was found after argonin and morphine. Also much red was present. Capsicum also gave a dark background. The color was strongly developed after iron, sugar, and lupulin. The *markings* were affected in much the same way as by cold and warmth. Reduction of the black or of the blue flecks occurred in some cases.

Pure Oxygen. — Pupæ kept in pure oxygen produced in the usual time butterflies normally colored and marked. Young caterpillars kept in oxygen took food for only one day, wandered about the next day, and died on the third or fourth day. The moist atmosphere rather than the oxygen may have been responsible for the early death of the caterpillars.

The Influence of Humidity on the Characters of Moths and Butterflies

Humidity is also supposed to have an effect on the coloration of butterflies. Marshall thinks that in the Transvaal, where a dry and a wet season alternate, as do summer and winter in northern climates, the seasonal dimorphism of certain butterflies is the direct result of the effects of moisture and of dryness, in the same way that cold and heat cause the seasonal dimorphism of northern species. Similar results have been described by Doherty for Melanites leda of India. The differences follow the dry and the wet seasons. Pictet has shown that effects of this kind can be artificially produced in certain European species. Moisture on the leaves produces great mortality

amongst the young caterpillars, but while the moths may be small their markings show no variations. On the other hand, although the fully formed caterpillars better resist the effects of moisture, aberrations in the color are produced. Thus when the caterpillars of Vanessa urticæ were fed for 8 to 10 days on leaves kept constantly wet, changes in the markings of the butterflies were produced. Similar results were brought about in Vanessa polychloros and in Hybernia defoliaria. In Ocneria dispar variations were induced in the first generation, but disappeared in the second, owing, Pictet thinks, to the caterpillars having adjusted themselves to the change, in the same way as they do to changes in their food. The variations induced in the first generation are very much like those produced by esparcette and dandelion, especially in respect to the males, and these plants contain a great deal of water in their tissues.

A fine spray of water at ordinary temperatures was constantly applied for 36 to 48 hours to caterpillars of Vanessa urticæ that had suspended themselves preparatory to changing into chrysalids. A marked effect was produced on the butterfly, a yellow band appearing across both fore and hind wings. The blue spots became gray or violet, and the border of the wings was clear. The variation resembles the variety polaris of this butterfly.

Humidity also acts on the chrysalid's stage, causing aberrations in a number of moths and butterflies. If the chrysalids are kept moist at a warm temperature, 30° to 35° C., very little effect is produced, because the development is so much hastened that the chrysalids pass through the critical stages before the protecting waxy covering is worn away. But if the chrysalids are kept cool while the moisture is applied, the effects are much more marked; for now the development is so much delayed that the water has time to penetrate the protecting coat and affect the critical stages.

Experiments with Flatfish

There are some experiments made by Cunningham with young flatfish which also show the effect of an external agent, viz., light, on the development of color. Very young fish were put into aquaria lighted from below. As the young fish underwent their metamorphosis, the pigment gradually disappeared on one side, as it does under normal conditions, *i.e.* as when they are lighted from above only. If, however, the fish are still illuminated from below, the pigment begins to come back again on the lower surface. The markings are similar in all respects to those on the upper side of the animal.

The result shows that the lower side of flatfish in their natural environment is white, because it is not exposed to light; but whether the result shows, as Cunningham believes, that the lower side has become white in the course of generations, because it has been turned away from the light, is not shown conclusively by the experiment.

Experiments with Crustaceans

There are a few cases, in other groups, where it has been shown that external agents produce *changes in form.* Branchippus ferox, inhabiting salt and fresh water, shows small differences in the length of the ovigerous sac, in the form of the segments of the body, in the length of the lobes that terminate the abdomen, and in the disposition of the abdominal bristles. Daphnia degenerata of salt water is only a degenerate variety of Daphnia magna of fresh water.

A species related to Daphnia — Moina rectivoctris — occurs in one form in fresh water and in another in brackish. The two differ in general points of structure due to the individuals becoming sexually mature before the final structural changes are completed.

The oft-cited case of Artemia may also be mentioned here. Schmankewitsch has described the slow transformation of Artemia salina into A. milhausenii, as the lagoon in which the

former was contained became more concentrated by evaporation. Experimentally he procured the same result by concentration. Furthermore Schmankewitsch claimed that by gradually diluting the brackish water in which Artemia salina lives he obtained a form having the characters of the genus Branchippus.

These conclusions have been seriously questioned by Bateson and by Samter and Heymons,[1] who have shown that Artemia salina is subject to great individual variability and that there is no close connection between the different variations and the concentration of the water in which they occur. Especially doubtful is Schmankewitsch's comparison with Branchippus, whose diagnostic features he seems to have imperfectly understood. Samter and Heymons find nevertheless that the salt content of the water has some influence on the form of Artemia salina, although in different pools of the same concentration a large range of variability exists. They think that other factors than concentration probably also affect the result.

Changes in Mammals and Birds

The Porto Santo rabbits, so fully described by Darwin, furnish another instance of influence of the environment. It is said that these rabbits originated from a single pregnant female that produced a litter on board ship in the year 1418 or 1419. Set free on the island of Porto Santo, the rabbits increased rapidly and soon became a pest. Darwin examined these rabbits and found that, compared with domesticated rabbits of average size, the Porto Santo rabbits had lost three inches in length and almost half the weight of the body. In other points also they differed — in the skull, and especially in color. "But here we meet with a singular circumstance: In June, 1861, I examined two of these rabbits recently sent to the Zoölogical Gardens, and their tails and ears were colored

[1] Schimkewitsch (*Biolog. Centralblatt*, XXVI, 1906) states that Anikin (1889) and Butschinsky (1901) have obtained results contradictory to those of Schmankewitsch. I have not seen their papers.

as just described (*i.e.* like the feral rabbits of Porto Santo); but when one of their dead bodies was sent to me in February, 1865, the ears were plainly edged, and the upper surface of the tail was covered with blackish gray fur and the whole body was much less red, so that under the English climate this individual rabbit had resumed the proper color of its fur in rather less than four years." [1]

Darwin thinks that "from the direct action of a humid climate and poor pasture the horse rapidly decreases in size in the Falkland Islands."

There is a great deal of evidence to indicate that climate acts directly in bringing about a change in the hair of animals, and not only is the thickness of pelt affected, but also the character of the hairs. Geoffroy St. Hilaire states that horses that have lived for several years in deep coal mines come to have a velvety hair, somewhat like that of the mole.

Wild ducks are said to change under the influence of domestication. The collar around the neck of the mallard becomes broader and more irregular. White feathers appear in the wings. The birds also increase in size, etc.

Certain foods affect the color of the feather of birds. Hemp seeds cause the color of bullfinches to become darker.[2] Wallace states that the natives of the Amazonian region feed the common green parrot with the fat of siluroid fishes, which causes it to become variegated with red and yellow feathers. How far these effects, produced directly by the environment, may become inherited will be examined in the next chapter.

[1] "Animals and Plants," Chap. V.

[2] Romanes, in his book on "Darwin and After Darwin," II, gives some further cases of this sort, p. 217.

CHAPTER IV

THE INHERITED EFFECTS OF CHANGES INDUCED BY EXTERNAL FACTORS

It has been pointed out that in butterflies the changes brought about by higher and lower temperatures give rise to forms that resemble southern and northern varieties of the same butterflies. The question at once arises whether species may not have originated in this way.

Fischer found that when a dark moth, produced by cold, was paired with another similar moth, the offsprings were also dark. His experiments extended, however, only to the first generation, and consequently the cold may have acted directly on the germ-cells of the parents. Highly important as this observation is in showing that the undeveloped germ-cells may be affected in the same way as the somatic tissues of the pupa, so that even under altered conditions the effect persists, yet the result as it stands does not conclusively show that permanent racial or specific changes have been produced in this way. Were such forms bred for several generations at a warmer temperature, it is possible that they would return again to their original condition. The new type might persist only so long as, or a little longer than, the external conditions are the same as those that produced it. The change may represent only an extreme fluctuating variation that has been caused by an external factor. The results do not appear, from this point of view, to belong to the kind of changes by which new species are made. Nevertheless the question still remains an open one as to whether changed external conditions may not at times cause more permanent effects. Some observations of Standfuss seem to show that such may be the case, although

the evidence is not satisfactory in all respects. He states that certain aberrations, that occur when the external factors have produced a sudden divergence from the parent form, are inherited. He shows by numerous experiments that these aberrant forms when crossed with the parent type do not give intermediate varieties, but that the offspring correspond to one or to the other parent. Thus the new type is not lost by intercrossing; but if adaptive, might perpetuate itself and form the beginning of new species.

The aberrations seem to resemble in these respects mutations. If they are really produced by a change in the environment, as Standfuss believes, the results throw most important light on the question of the origin of mutations — a question which at the present time is one of the most pressing questions of the theory of organic evolution.

Standfuss believes that effects of these kinds are inherited, and that new species may be evolved at the limits of the range of forms through the effect of external agents. It is not quite clear to me, how he supposes such results come about, since his own experiments seem to show that the effects of moderate changes in temperature are only temporary. He appears to believe, however, that the effects, if long enough carried out, become in large part fixed.

In plants the effects of the environment on the form, growth, and time of flowering have long been known; and many experiments have been made by transporting plants from one locality to another. It has been shown that many alpine plants will flourish in the valley, and often great changes in the character of the plants have been noted. Naegeli has carried out elaborate experiments of this sort. He collected in the Botanical Garden of Munich 2500 varieties of mountain plants, and for several years made observations on the effects of changes in the environment. The changes are seen at once, showing that no permanent effects have been produced by the alpine climate. Other botanists, however, claim that for a time at least the effect of the original habitation may be seen.

Pictet, as has been shown in the preceding chapter, has also obtained direct evidence of the inherited effects of food. It should be noticed in this case that the young caterpillar fed on the leaves of a new food plant produces changes of a certain type in its somatic cells that appear in the butterfly. The caterpillars of these butterflies, reared on their natural food plant, produce butterflies that also show evidence of the effect caused in the preceding generation. It is probable that this influence was directly induced in the germ-cells of the first generation, so that the effects were not inherited through the soma, but were directly produced. The point, however, of special interest in these cases, aside from the question of inheritance, is that the influences that induce certain changes in the somatic cells of the caterpillar affect the germ-cells of that caterpillar in the same way, so that when they develop they, too, give the same results. The effect is weakened, it is true, in the second generation; but this may be due to the counteracting influence of the normal food. The results show that the influence of the environment may persist for one or more generations in another environment.

Recently de Vries has dealt with the same subject, and has carried out certain experiments that bear on the question. He believes that in general the effect of the environment produces only the fluctuating variations seen in plants. The full effects may not appear at once, but may be accumulated, through several generations, and hence would seem to be inherited. He speaks of these changes as acquired characters, and believes, as I have said, that individual variations are simply acquired characters due to differences in the environment. We are to understand, however, that de Vries means that these characters are acquired either by the somatic cells or by the germ-cells, but independently of each other, *i.e.* the effects acquired by the somatic cells are not supposed to affect the germ-cells except indirectly, namely, by affecting the nourishment of the germ-cells.

The question arises whether these new characters are inherited

when the environment that has caused them is altered. De Vries answers this question in the following way: If the seeds of the best-nourished ordinary plants are selected and planted under the most favorable conditions, the average plants of the next generation will not only be as vigorous as the former, but their seeds themselves will have a higher average of size. If this process is continued, the average of the race will be increased in the direction of selection, and in time the race, *i.e.* all the individuals, may be brought to and maintained near the highest plane to which fluctuating variation ever reaches.

There is a counteracting principle that must also be considered, viz., what Galton has called regression toward mediocrity. If variations that depart from the average of the type are united, their descendant will tend in some degree to return to the average or to mediocrity, as Galton has shown. If, however, we pick out in each generation those that are most above the average, the average of the descendants in each generation rises, despite the regression, and in time the average may be brought near to the highest point to which individual variations reach. In other words, the character that appeared in the first generation as a somatic variation of one individual has become temporarily transferred to the seeds; but unless the same favoring external conditions are vigorously maintained, there will be a return to mediocrity.

This fastening, as it were, of the individual variation upon the race is due, de Vries thinks, to the action of the nourishment on the germ-cells.

If a plant is well nourished, it produces larger seeds that are better supplied with nourishment. Hence on an average they will give rise to more vigorous plants, and these in turn will produce an average of larger or at least of better-nourished seeds, and the plants from these will be still stronger. Thus by slow degrees the seeds acquire the same sort of characteristics as those shown by the best-nourished plants in any one generation. The curious thing about this is that the seeds do not respond completely in the first generation, but it takes sev-

eral generations to produce seeds *all* of which contain nearly the maximum possible food supply.

Suppose when this condition is attained we reverse the process and plant the seeds under poorer conditions. The first crop from such seeds will still be above the original average, but not as much above as though they had grown under favorable conditions. Their seeds again will contain less nourishment, and the second generation will be still smaller on the average, until finally the race reaches the lowest level shown by fluctuating variations.

The inheritance of the acquired character in these cases is brought about in rather a peculiar way. The favorable external conditions, for instance, act favorably on the body-cells of the plant, and the germ-cells are therefore well nourished and store up more food: not all to the same extent, but the average is higher than in the preceding generation. The next generation thus gets a better start, and if the plants are better nourished than the average, a similar advance is again made. We must not forget that in each generation some of the seeds may be as good as the best, but others are not as good. It is the average that is improved, and not the best individual seed.

It may appear from the case just given that the food conditions determine only the size and vigor of the plant. This is not the whole matter, for even the characters of certain parts may be changed in a plus or a minus direction, provided they are correlated with the condition of nourishment of the plant. De Vries cites the case of the poppy, Papaver somniferum. In this plant the stamens may be changed into supernumerary or accessory carpels by changing the external conditions. The number of these carpels may be as great as 150 or more. From the seeds of flowers with an average crown of carpels, plants may be reared having many or few of these organs. The more favorable the conditions, the more numerous the carpels, and *vice versa*. Poorly nourished plants may have only one or two rudimentary or accessory carpels.

If we select in each generation the most vigorous plants (hav-

ing, therefore, a high average of carpels), and keep them under favorable conditions, the average of carpels of the race can be temporarily increased. Conversely, if we select the less vigorous plants, and put them under unfavorable conditions, the accessory carpels can be made to disappear.

This connection between individual vigor and the formation of carpels is not an absolute one, for there are means by which vigorous plants can be obtained without accessory carpels. If very young plants are transplanted, and then put under favorable conditions, vigorous plants result without or with few carpels. The interpretation that de Vries gives of this result is that the flower buds were not laid down at the time of transplanting, but develop soon afterward, when the conditions are temporarily unfavorable. Later, when the favorable conditions begin to act, the rest of the plant responds, but it is too late to affect the carpel formation.

It will be observed that we are dealing here with rather a special case, viz., that of nourishment alone. Somatic cells and body-cells alike are affected in the same way. If along with this condition of nourishment there are certain correlated changes, such as the formation of accessory carpels, the principle remains the same. The point of special interest is that the effects may be accumulated only slowly by the seeds, so that it takes several generations to produce the best average effects. The effect, once produced, may persist in part through several generations subjected to the reverse conditions. The results are not unlike those in the butterflies, in which the effects of temperature or of feeding are marked in the first generation, and then decline if the external conditions that produced them are changed.

It is difficult to reach any probable conclusion from the evidence given in the preceding pages in regard to the inherited effects of the influence of the environment. Possibly we are dealing with two distinct problems. In most cases the effects on the body-cells and on the germ-cells are only temporary, and persist only as long as, or a little longer than, do the condi-

tions that called them forth. The result is only a special case of the inheritance of fluctuating variations. On the other hand, in some of the cases of aberrations given by Standfuss, it appears that a permanent change has been brought about by the environment which persists afterward, independently of the influences that caused it. What is still more interesting is that the new characters may be transmitted to the offspring formed by a cross between the new and the parent type. We shall consider this question at greater length in a later chapter.

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CHAPTER V

THE INHERITANCE OF ACQUIRED CHARACTERS

In the preceding chapters we have seen that *external* factors may cause definite changes in the form, color, markings, etc., of animals, as well as certain changes in plants. The question arose whether these effects are transmitted to the offspring of the next generation. An examination of the evidence seemed to show that in most cases the effects are inherited only in so far as the germ-cells are also affected by the external factors.

It has been long recognized that *internal* factors also may cause changes in animals. The use of an organ may increase its size, and also its effectiveness, even when the change in form is so slight as to escape notice. Here, also, the question arises whether these effects are inherited. Disease or injury may bring about changes in an organ, and again the question has been raised as to whether the effects are transmitted to the offspring.

The phrase "the inheritance of acquired characters" is used to include supposed cases of inheritance of these different kinds of effects; and it is customary to use this term to include also cases like those described in the last chapter, in which the external agents act directly on the germ-cells, as well as on the body-cells. In this chapter I shall use the term in a restricted sense, and include under it only those cases in which the body-cells are first affected and are then supposed to transmit their influence to the germ-cells.

It is not necessary to consider at length the historical origin of the idea that acquired characters are inherited. It is well known that Lamarck based his theory of evolution on this

assumption, not only in the restricted sense as defined above, but also in the sense that external conditions may directly affect the whole organism, *i.e.* germ-cells as well as the body-cells. He made no such sharp distinction, however, between these two sides of the question as we find it convenient to make nowadays.

Let us examine critically the experimental evidence on which the theory of the inheritance of acquired characters, in the restricted sense, rests, for, could it be shown that changes acquired through use are transmitted to the next generation, we might seem to be able to explain how many of the complicated adaptations and coördinations of animals have arisen.

Amongst modern writers the first to seriously question the truth of the generally admitted doctrine that acquired characters are inherited was August Weismann. In his essay "On Heredity," published in 1883, and in two subsequent papers "On the Supposed Botanical Proofs of the Transmission of Acquired Characters" (1888), and "The Supposed Transmission of Mutilations" (1888), Weismann challenged the accepted point of view. His conclusions have become common knowledge, so that it will not be necessary to go over the ground again. While many zoölogists and botanists were convinced by Weismann's argument, which seemed to show that the evidence fails to support the view that acquired characters are inherited, a few zoölogists have always insisted nevertheless that such characters are inherited, and a few investigators have brought forward experimental evidence which they believe shows convincingly that changes brought about in the body may be transmitted to the germ-cells. It is this experimental evidence that I propose especially to consider.

Darwin believed that acquired characters are inherited, and in the "Origin of Species," in the "Animals and Plants under Domestication," and in the "Descent of Man" he accounts for many adaptations in this way. Herbert Spencer, especially, although not always with discrimination, used this hypothesis to account for many structures and habits of animals and plants.

I do not propose to consider in detail the cases that Darwin and Spencer have brought forward (most of them will not bear critical examination, as Weismann has so ably shown), but, as has been said, I shall consider rather those cases, most of them recent, in which attempts have been made by direct experiment to show that acquired characters are inherited.

The work that has attracted most attention is that of Brown-Séquard. A full statement of Brown-Séquard's experiments and results is given by Romanes in his book "Darwin and After Darwin," Vol. II, Chap. IV. The experiments were made with guinea pigs. Epilepsy was induced by operations on some part of the nervous system. The young of these animals sometimes developed epilepsy, or some of its effects, in the same part of the body as that affected in the parent. The details of the experiments are as follows: The parents became epileptic after injury to the spinal cord or by section of the sciatic nerve. The "epileptiform habit" does not supervene until some time after the operation and lasts only "for some weeks or months." The convulsions "never occur spontaneously, but only as a result of irritating a small area of skin behind the ear on the same side of the body as that on which the sciatic nerve had been divided." [1] The attack lasts only a few minutes, and during this time the animal is unconscious and convulsed. The habit is only rarely transmitted to the young, but as the disease occurs only in guinea pigs whose parents have been made epileptic by an operation of the sort described above, and never in the young of guinea pigs that have been operated on in other ways, there seems to be here something more than a coincidence.

Another series of experiments consisted in cutting the cervical sympathetic nerve. This operation causes a change in the shape of the ear, and a similar change is said to appear in the young. By cutting the cervical sympathetic nerve or by removing the superior cervical ganglion, the eyelids partially close, and this closure was also seen in the young.

[1] Romanes, "Darwin and After Darwin," II, 1895.

If a particular spot of the restiform body of the brain is injured, a marked protrusion of the eyeball quickly follows. The progeny of parents thus affected show also an abnormal protrusion. Romanes also observed this, but he found that the young show less protrusion than do the parents, and since the amount of protrusion of the eyeball is variable in normal guinea pigs, Romanes is not certain that there is anything more than a *coincidence* in the cases that he observed.

An injury to the restiform body may also cause dry gangrene (and hæmatoma) in the ears. This disease may appear either several weeks after the operation or even later. It affects, Romanes says, usually the upper parts of both ears and may gradually "eat its way down" until two thirds of the tissues of the ears are affected. In the offspring from animals of this sort a morbid condition of the ears may arise at any time in their lives, even after they have become full grown. The disease does not go so far as in the parents, and "almost always affects the middle third of the ears." Romanes points out that this particular disease never appears amongst guinea pigs unless their own or their parents' restiform bodies have been injured. Furthermore, he tested the possibility that the results are due to contagion by inoculating "corresponding parts of the ears of normal guinea pigs by first scarifying those parts and then rubbing them with the diseased surfaces of the ears of mutilated guinea pigs." The disease was not communicated in this way.

Brown-Séquard found that after cutting the sciatic nerve (or this and the crural also) the leg became anæsthetic, and the guinea pigs would sometimes eat off two or three of their hind toes. In the offspring of these animals he found sometimes an absence of toes, or only a part of one or more of the toes might be missing. The inheritance occurred in only one or two per cent of cases. Romanes, who repeated the operation through six successive generations, never obtained any results.

Another outcome of injury to the sciatic nerve is to induce "morbid states of the skin and hair of the neck and face in

animals." This result is also said by Brown-Séquard to be inherited.

I have given somewhat fully these remarkable results of Brown-Séquard because the experiments appear to have been carried out with such care, and the results are given in such detail that it seems that they must be accepted as establishing the inheritance of acquired characters.

Moreover, similar results have been obtained by other investigators. They have been corroborated in part by Obersteiner.[1] Westphal has produced epilepsy by striking the heads of the animals with a hammer, and has found that the young are often epileptic.[2] Still more important are the experiments of Romanes. His conclusions, it is true, are much more cautious, and his statements more guarded than those of Brown-Séquard; yet on the whole they confirm Brown-Séquard's claims.

Weismann has attempted to discredit these results on the ground that we are still ignorant of the cause of epilepsy. The possibility that it is a bacterial disease must be admitted, he claims, and, if this is the case, the bacteria themselves may be transmitted to the young during their uterine existence. It is supposed, in fact, that other diseases may be inherited by direct contagion through the germ-cells of the father or the mother. This objection is, however, purely formal, and as long as we do not know that epilepsy is a bacterial disease that is contagious in the way supposed, the objection may raise a doubt but cannot set aside the results.[3]

There are some quite recent experiments that may have a very direct bearing on the questions here raised. In a paper by Charrin, Delamare, and Moussu, the inherited effects of injury are described. The liver or the kidneys of pregnant rabbits and guinea pigs were injured, which caused these organs

[1] *Oesterreichische medicinische Jahrbücher*, p. 179, 1875.

[2] See Weismann, "Essays," Vol. I, p. 323.

[3] It has also been suggested by some more recent authors that epilepsy occurs as the result of a weakening of the general condition either direct or inherited. This view will not explain the localized inheritance claimed by Brown-Séquard.

to become diseased. The offspring sometimes showed defects in the corresponding organs. The authors suggest that some substance may be set free from the diseased organ which may be carried in the blood, and by diffusion get into the blood of the embryo, and directly affect the development of the corresponding organ. They attempted to test this hypothesis by injecting into the blood of a pregnant animal extracts from the diseased kidney of another animal, and while the authors do not appear so certain that similar effects are here also produced in the organs of the embryo, yet this seemed to be the case.

It will be observed that this transmission of an acquired character, if it really occurs, appears to be different from that of transmission through the egg, for it is the developing organ itself that is acted upon.

These results may possibly have a bearing on Brown-Séquard's work, since they seem to show that if an organ of an adult animal (that is viviparous) is diseased, the same organ of the young may develop abnormally (or become diseased). Whether the two cases are really the same we do not know. In fact, it would be extremely hazardous to conclude even that they may be, until we know in what way epilepsy is caused — whether by a physical defect in the nervous system, or by bacteria, or by some other means. It should not be overlooked that the epilepsy was not present in the young when born, but developed later. There is urgent need that experiments of this sort be carried out on an extensive scale.

Many other cases of mutilations have been cited to show that acquired characters are inherited. Defects in the parents are said sometimes to reappear in the young, and it is inferred that in some way the two things are connected. We are apt to overlook the fact that thousands of injuries are not inherited, and that a malformation appearing in the child in the same organ that had been injured in the mother or father may chance to occur at any time, and would be certain to arrest attention. We might err if we concluded in such cases that

there was any direct connection between the conditions in the parent and in the offspring.

On the other hand, if the results of Charrin, Delamare, and Moussu are confirmed, there is a chance that *diseased* organs at least may affect the young *in utero*. This would, of course, only allow the inheritance of acquired characters from the mother, and not from the father. This difference might give us a chance to test the view that the effects are produced in the embryo *in utero* and not in the germ-cells. It is interesting to note that Brown-Séquard found that epilepsy is more often transmitted through the mother than through the father. In the case of mutilations, the injury may have been inflicted years before, and the wounds have completely healed before the young are conceived; yet cases of this sort have often been cited to show inherited effects. In such cases it is difficult to see how such effects could become transmitted, especially through the male.

Weismann has given in the "Essays" referred to above an interesting and very full discussion of the supposed cases of inheritance of acquired characters. He himself carried out some experiments with mice. For four generations the tails of mice were cut off. Of the 901 mice born during this time not one had a short tail, and careful measurements showed that there was no shortening at all of the tail of the offspring. This experiment was, it is true, almost needless, since it is customary to cut off the tails of certain breeds of sheep and the ears of dogs without these breeds ever having become tailless or earless, and circumcision has been practiced in man for centuries without any appreciable effect.

Since in these cases the organs operated upon had healed over before the next generation was born, there would be little chance of the injury directly affecting the embryos. Moreover, even if such effects are inherited, it might not follow that the tails would be shortened, but at most only diseased in some way.

Recently Nussbaum has commented on this side of the ques-

tion. He claims that we should not expect the inheritance of short tails, because even if such an influence were transmitted to the egg, the young embryo would promptly regenerate its missing portions. Unfortunately there is no evidence that they can regenerate in the embryo.

It has been claimed that the removal of or injury to an organ is a different process from the modification of an organ caused by some external condition. There are, however, cases in which an organ has been greatly modified for several generations and no inherited effect has been produced. The feet of Chinese women are compressed so that their form is greatly changed, and in the higher classes this has been kept up for generations, yet no effect has been produced on the feet of the children. Certain races of Indians are known to have changed the shape of the heads of their children by compressing them between boards, yet the effect does not seem to have been inherited. Tight lacing may change very greatly the shape of the ribs and to some extent the position of the viscera, yet no inherited effect has been produced.

We may now consider the cases of the supposed inherited effect of use and of disuse. We are familiar with the decrease of a part in size and in function through disuse, in the case of muscles, glands, bones, etc., and also with the enlargement of organs through use. It is especially this class of facts that impressed Lamarck, and which led him to assume that these effects are inherited. The rudimentary eyes of animals living in the dark are often cited as having resulted from disuse. The long neck of the giraffe and the long tongue of the ant-eater, of humming birds, and of woodpeckers are examples, that Lamarck has given, of effects produced by use; and many naturalists since Lamarck's time have cited these and other similar cases as bearing on the question. But neither Lamarck nor his successors have been able to demonstrate by experiment that the effects of use and disuse of this kind are inherited by the next generation, and until this proof is forthcoming we must regard their view as purely speculative. It is surprising

that no experimental proof of this kind has been furnished, because it would seem that it ought not to be difficult to make crucial experiments that would settle the question at once. It is true that many of the latter-day Lamarckians claim that effects of this sort are only very slowly brought about, and that we should not expect to observe any results that are measurable in the course of a few generations. It seems to me that by taking this position the Lamarckians distinctly avoid the real issue; for it is not evident why such effects, if produced at all, should not appear at once in the embryo, since they appear at once in the adult.

It is evident that if the effects of use and disuse were inherited, many of the adaptations of organisms to their surroundings could be quickly attained; for the parts most used would be strengthened in successive generations, those less used would soon decrease in proportion to their use, and the complicated adjustments of the different parts could be accounted for. The habits and instincts of animals would also be made to conform to the needs of the animal. These benefits are so obvious that it is small wonder that the theory of the inheritance of acquired character has always had its adherents. But the plausibility of a theory is not a scientific proof of its worth, and the best evidence, viz. that from experiment, that we have at present, does not show that acquired somatic characters are inherited through the germ-cells. Moreover, the advocates of the theory overlook a consideration of prime importance. If the effects of mutilations and of diseases are also inherited, the results would be highly injurious to animals. Considering how often animals are injured, we should expect to find the animal kingdom in a most dilapidated condition if the accidental injuries of all their ancestors were transmitted to subsequent generations. It is unfortunate that many of the best-authenticated cases of the inheritance of acquired character are those relating to disease.

In recent years two elaborations of the principle of inheritance of acquired characters have appeared. Semon has worked out Hering's original suggestion that heredity is racial mem-

ory. Under the title of "Die Mneme," Semon has analyzed and classified the different forms of inheritance of former experiences of the individual which are assumed to become in time the herditary capital of the race. Rignano has developed the idea of the influence of the germ-cells on the soma, and *vice versa*, from a different standpoint, viz. that the germ-cells influence the soma during development and in turn are at times influenced by the soma. These speculations are based on the assumption that acquired characters are inherited. Since we are concerned here only with the experimental evidence in favor of or opposed to this assumption, it would carry us too far to attempt to deal critically with these elaborations, that assume at the starting point that such characters are inherited.[1]

Telegony

We may next examine the evidence that has been supposed by certain writers, in the main "practical" breeders, to prove that maternal impressions of various kinds can be transmitted to the young *in utero*. The crudest examples are those in which it is related how the pregnant mother, being impressed by some unusual or revolting sight, has transmitted to her infant a corresponding structural deformity. Somewhat less credulous perhaps are those breeders and "fanciers" who are firmly convinced that if a purely bred animal — the horse and the dog are the stock examples — has first been paired with a mongrel animal, the subsequent offspring to a purely bred father will show evidences of the first birth, *i.e.* be impure as to their breed.

The credulity of men who have not been trained as to the value of evidence is a matter of everyday observation, and it is not going too far to say that most opinions or statements of the "practical" breeder must be put to a rigorous scientific test before they can be trusted. This has proven to be the case with telegony.

[1] For a criticism of Semon's argument, see Weismann's recent (1906) review.

The best-known case, and one that Darwin himself believed to have been "perfectly well ascertained," is that of Lord Morton's mare, a full account of which is given in Darwin's "Animals and Plants." A pure Arabian mare was bred to a quagga, and the first offspring was, of course, a hybrid. The second time, the mare was bred to a stallion of pure stock. The colt showed cross markings on the legs, that were *said to be* much more developed than on colts of pure pedigree. Darwin thought the evidence sufficient to show that in some unknown way the mother had been affected, either by the sperm of the quagga or by the hybrid embryo *in utero*, and this effect was again in some unknown way transmitted to the second offspring. Darwin advanced this case as one of several in support of his hypothesis of *pangenesis*.

The statements remained practically undisputed until within recent years. A few years ago Ewart undertook to repeat the experiment, which he was enabled to do by having a small experimental farm placed at his disposal. Careful series of cross-breeding experiments, followed by pure breeding, were carried out. Ewart discusses his results in his book entitled "The Penycuik Experiments," and reaches the conclusion that no clear evidence of infection, if I may so call it, can be produced in this way. He also points out that it is not uncommon for colts, purely bred, to show stripes as distinct as those in Lord Morton's case. Fortunately a picture of this colt is still in existence, and its examination shows that the markings are not more distinct than those that sometimes occur in the case of purely bred animals. There was, then, merely a coincidence, and not a causal connection.

Bell has given an excellent summary of the evidence in regard to the possible influence of a previous sire, and has carried out a number of experiments on horses and dogs.[1] In none of these cases was any influence of the previous progeny or of a

[1] Two other cases were reported to Bell, one for pigeons and the other for a cross between a negro and a white woman. In neither case were the later offspring, by a father of their own kind, affected by the first union.

previous sire to be seen in the later offspring. The experiments were made with pedigree stock, and the results are convincing, and indicate that the belief in an influence of this kind is another breeders' myth. Minot has also obtained negative evidence with guinea pigs, and I have obtained similar negative evidence with mice.

Xenia

It has been claimed that in plants the influence of the pollen is sometimes shown in those parts of the fruit or of the seed that are derived from the mother plant.[1] The flower of the orange, fertilized accidentally by pollen from the lemon, is said sometimes to produce fruit that may show a stripe in the peel like that of the lemon, although the peel is a product of the tissues of the mother plant. Similar cases have been recorded for the seed-color, and even for the pods of peas. The most familiar case is that of the color of the grains of maize.

In recent years it has been shown that some, at least, of these cases can be explained as the result of a process of double fertilization. It has been found that there enters the embryo sac not only the sperm-nucleus, that unites with the ovum, but another nucleus that fuses with the "polar" nucleus or nuclei. The latter combination gives rise to the endosperm, which is therefore hybrid in origin, and may show the influence of the sperm nucleus if this contains the dominant character.

In regard to the other cases, where the color is not in the endosperm, the results cannot be ascribed to the sperm nucleus. Giltay, who has made some experiments to test this point in peas, found no instances where the color of the pods could be assigned to the influence of pollen plant.[2]

Theories of Transmission of Somatic Influences

The only theory of any prominence that pretends to indicate how changes in the somatic cells may affect the germ-cells is

[1] From the nature of the case the process could not be expected to occur in animals.

[2] See Davis, B. M., *American Naturalist*, XXXIX, August, 1905.

Darwin's provisional hypothesis of pangenesis. Many of the assumptions of this theory are scarcely in accord with our present cytological knowledge. For instance, few cytologists would be likely to admit that the germ-cells are built up of living particles representing the different tissues and organs of the body that are collected by the reproductive organs. In a modified form, however, Darwin's hypothesis could no doubt be brought up to date, if it were desirable to do so; but is it worth while to speculate further in this direction until we have a better basis of fact on which to rest the speculation; for, as has been pointed out, the experimental evidence in favor of the inheritance of acquired characters is unsatisfactory?

The idea that the cell is made up of smaller morphological units that represent the various potentialities of the cell has been a favorite assumption of modern writers. Thus we have the physiological units of Spencer, the gemmules of Darwin, the pangens of de Vries, the plasomes of Wiesner, the micellæ of Nägeli, the plastidules of Haeckel, the biophores of Weismann, the biogens of Verworn, the idioblasts of Hertwig, etc.

It is perhaps needless to point out that the kind of reasoning on which this method of treating the problem of heredity rests is of the sort that gives only the appearance of a real explanation, for the responsibility is only shifted to invisible and imaginary units that can be worked like puppets, at the will of the philosopher. Grossly ignorant as we are concerning the chemical and physical basis of cell activity, it is not probable that such guesses can be much more than fictions or at most symbolic.

A single citation from Darwin will serve to bring the main points of his theory of pangenesis before us. "It is universally admitted that the cells or units of the body increase by self-division or proliferation. . . . But besides this means of increase I assume that the units throw off minute granules which are dispensed throughout the whole system, that these, when supplied with proper nutriment, multiply by self-division, and are ultimately developed into units like those from which they were originally derived. These granules may be called *gemmules*.

They are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms a new being. . . ."

A few experiments have been made to test this view. Galton[1] transfused the blood of one variety of rabbit into the veins of both sexes of another species, and then bred together the latter. If there are gemmules in the blood, the germ-cells of the rabbits containing the transfused blood might possibly show the influence of the other variety. No evidence of such an influence was found.

Darwin did not admit that this experiment was decisive, and Galton himself admitted that the results are not convincing. Darwin thought that the few gemmules present in the blood at any one time might not succeed in supplanting the similar kinds of gemmules supposed to be already present in the germ-cells.

Another experiment was carried out by Romanes. Wild rabbits supplied the blood, and Himalayan rabbits received it. Several transfusions were made. In one case the blood of three wild rabbits passed through the veins of the domesticated individual. No evidence of any "foreign" influence was found in the offspring. Romanes said later that he had discovered that this experiment could not have been expected to give any positive results, because rabbits when crossed do not produce young having intermediate character. The force of the admission is not very convincing, however, for the offspring might still have been expected to show the effects — if such influences are transmitted in this way — of the dominant breed, if this had been used to supply the transfused blood. Moreover, Castle has shown that in some breeds of rabbits certain characters at least are intermediate in the hybrid — the length of the ears, for example.

Other zoölogists who have refused to accept the doctrine of the inheritance of acquired characters — Weismann, for instance — have nevertheless used another idea contained in Darwin's

[1] Proc. Roy. Soc., 1871.

hypothesis. The elementary characters of the cell are assumed to be contained in minute, living elements, gemmules, pangenes, etc., that multiply and increase independently of each other; but their migrations are now limited to the individual cell. The nucleus is believed to be the storehouse of these units that issue forth at times to perform any function whatever that may be assigned, *pro tem.*, to the cell. De Vries's theory of intracellular pangenesis rests on this assumption. How such bodies eat up or replace the rest of the cell contents to dominate its function we are not told, and details of a chemical nature are deplorably lacking. Since this army of immigrants is confined within the boundaries of the cell, they have no importance to us in this connection. The historical origin of the ideas in regard to these bodies is, however, not without interest here. The superficial analogy between the theory and that of the atomic theory of the chemists has sufficed to lure many writers into this fascinating and facile mode of speculation.

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CHAPTER VI

EXPERIMENTAL HYBRIDIZING

WITHIN the limits of the Linnæan species it has been found that varieties, or races, or breeds, are generally perfectly fertile when crossed, and in recent years these fertile crosses have been much studied. In some cases it has been found that a character that is different in two parents blends in the offspring, and may or may not separate again; in other cases, however, a character that differs in the parents does not blend, and all the offspring of the first generation are like one of the parents. The inheritance is alternate. If hybrids of this kind are bred to each other, the original character of one of the grandparents may reappear in some of the offspring, the contrasting character of the other grandparent in others. These cases follow what is known as Mendel's law.

It is sometimes stated that Mendel's law applies only to crosses between varieties, and this is true for many cases; but characters that are entirely new to the race may also follow Mendel's law; and if the appearance of one new character suffices to characterize a new form as an elementary species, we must conclude that the characters of some elementary species also follow Mendel's law of alternate inheritance.

Mendel's Law

In 1865 Mendel published the results of an elaborate series of experiments that he had made with varieties of peas. It is strange that so important a discovery should have been entirely neglected for thirty-five years, especially since the question of

heredity and evolution were being actively discussed during that time. It was not until 1900 that de Vries, and simultaneously Correns and Tschermak, independently obtained results that brought to light again the long-forgotten discoveries of Mendel.

Mendel found that when the flowers of one race of peas are fertilized artificially with pollen from another race, the hybrid offspring (F_1) of the first generation are like one of the parents in each particular character, and not intermediate in character. If, however, these hybrids were self-fertilized or inbred, both grandparental types reappeared in their offspring (F_2), and in definite proportions. The character of one of the parents that appears in the first hybrid generation (F_1) is called the *dominant*, and the contrasted character of the other parent that disappears in the first hybrid generation is called the *recessive*. When these first hybrids are inbred as stated above, there appears in the second generation of hybrids (F_2) three individuals showing the dominant character to one individual showing the recessive. This, however, is by no means the whole discovery; for Mendel found that the recessives of this second generation, if inbred, give always recessives and nothing else. Those that show the dominant character, on the other hand, do not all breed true. A third only are pure and give rise only to dominants, while two-thirds of them produce both dominants and recessives. The matter can be graphically expressed as follows: —

If we call the dominant character A, the recessive B, then the first generation (F_1) of hybrids will be $A(B)$. This means that while the hybrids show outwardly only the dominant character A, the recessive character (B) is also present in an undeveloped condition. When these hybrids (F_1) are inbred, the A-character dominates in one fourth of the offspring, the B-character in one fourth, and the $A(B)$ character in two fourths, *i.e.* in the proportion of 1 : 2 : 1. Mendel showed by a simple

[1] In practice $A(B)$ can only be distinguished from A by the kind of progeny that each produces.

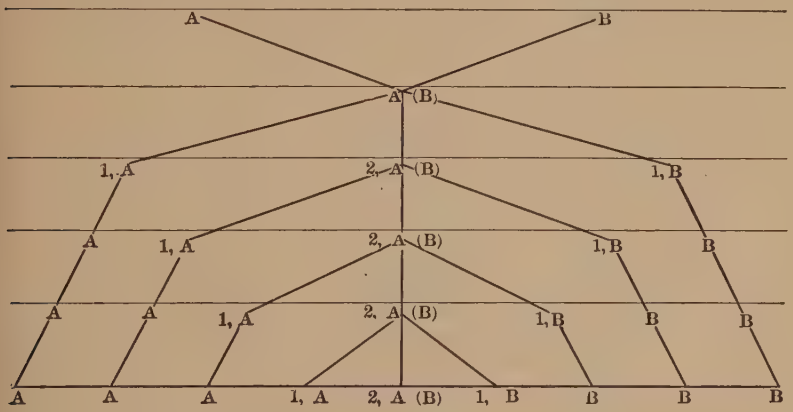
assumption how this numerical relation could be explained. When the male, *A*, and the female, *B*, *germ-cells* unite, every cell of the hybrid will contain both *A* and *B*; in which case one dominates, namely, *A*, giving *A*(*B*). If we assume that in the *germ-cells* of the hybrid the characters *A* and *B* separate again, and go to different cells, half of the germ-cells will contain the one character only, and the other half the other character. This is supposed to take place both in the male and in the female individual. The male germ-cells containing *A* may meet egg-cells containing *A* or *B*, and conversely the male-cells *B* may meet egg-cells containing *A* or *B*. The possible combinations that result are shown in the following diagram: —

The chances are that, on the average, *A* will meet *B* twice as often as *A* meets *A*, or that *B* meets *B*. Hence the combination *A*(*B*) will occur twice as often as *AA* or *BB*. The outcome will be 1 *AA*, 2 *A*(*B*), 1 *BB*. Thus according to the assumption of *two kinds of germ-cells in the hybrid* the numerical results agree with the actual results of the experiments. For this reason Mendel's assumption of two kinds of gametes has been generally accepted. Furthermore the theory can be tested in several ways, as will be shown later, and it has so far, on the whole, stood the test. When in addition to this it was found that in the germ-cells a mechanism exists that seemed capable of carrying out the postulated process of purification, it appeared to a number of modern zoölogists that Mendel's assumption of two kinds of germ-cells in hybrids of this sort is a real and not a fictitious explanation of the results.

An actual example may make clearer Mendel's principle and its interpretation. If a gray house mouse, *A*, is crossed with a white albino mouse, *B*, the offspring, (F_1), will be all gray like the house mouse. If these gray hybrids[1] (F_1) are bred to each

[1] Following Mendel the cross between two races or varieties is called a hybrid, although this term has been usually employed for crosses between species.

other, their offspring (F_2) will be gray or white in the proportion of 3 : 1. If the white individuals are inbred, they will give only white, and this is true for all of their descendants. They are said therefore to be "pure." The gray individuals, however, show themselves to be of two kinds; one third of them, if inbred, produce only gray, and all of their descendants will be gray. They, too, are said to be "pure." The other two thirds, if inbred, produce both white and gray mice. If these offspring are examined by further crossing, it is found that the whites are pure and give only whites; that some of the grays are "pure" gray, but the others are gray-dominant-white-recessives, $A(B)$, and again in these we find the proportion 1 A : 2 AB : 1 B. The following scheme will show at a glance the succession of generations: —



A practical consideration of some importance is obvious from these results. Pure races can be obtained from the hybrid, $A(B)$, by selecting the offspring with "pure" germ-cells, A or B. On the other hand, the $A(B)$ hybrids always produce some $A(B)$, so that all their offspring do not return entirely to the two parental types, but in every succeeding generation they will continue to split off some "pure" A's and B's.

As has been stated, Mendel's assumption in regard to the two kinds of germ-cells has been tested in other ways and found to

conform to expectation. One way has been to breed back the first hybrids $A(B)$ to the parent form, either A or B; the other way has been to apply the rule to more than one character. These two methods may now be illustrated.

If a hybrid, $A(B)$, is bred back to the parent type, B, half of the offspring should be $A(B)$ and half BB. This must occur because, on the assumption, the germ-cells of $A(B)$ are A and B, while those of BB are B and B; thus —

A	B
B	B
$A(B)$	BB
$A(B)$	BB

If, on the other hand, $A(B)$ is bred back to the other parent type, A, all the offspring will be like A, although only half are pure A's, the others being $A(B)$; thus —

A	B
A	A
AA	$A(B)$
AA	$A(B)$

The most interesting test that Mendel made of his theory involves the heredity of two dominant characters and two recessive characters. Thus, if two varieties, AB and ab, are crossed, the first hybrids (F_1) will be $AaBb$. Since A and B dominate, these individuals will all resemble AB externally.

The germ-cells of the hybrid individual, $AaBb$, will be of as many kinds as there are possible combinations of A, a, B, b, *provided* that each combination contains some A (or a) and some B (or b), *i.e.* one or the other kind of the two characters, Thus the only possible combinations are AB, Ab, aB, ab.[1]

[1] It may seem that these four combinations do not exhaust all the possible combinations of the letters, because AA, Aa, aa, BB, Bb, bb, might be supposed to appear, but this is not the case, because on the assumption of paired characters A (or a) must always be accompanied in the germ-cell with B (or b) characters. Similarly, B (or b) must always be accompanied by A (or a) characters. Hence the six combinations just given are excluded.

Each of the four kinds of egg-cells may be met by any one of these same four kinds of male cells, giving in all nine combinations; viz. *AABB*, *AABb*, *AaBB*, *AaBb*, *AAbb*, *Aabb*, *aaBb*, *aaBB*, *aabb*. But since these are combinations of both dominant and recessive characters, the offspring will appear to be of only four kinds. Thus the first four terms will belong to the type *AB*; the next two kinds will be *Ab*; the next two *aB*; and the last *ab*. It will be found by making all the possible combinations that the *AB* type occurs nine times, *Ab* three times, *aB* three times, and *ab* only once.

Mendel carried out an experiment of this sort in which two contrasted characters were involved. The results fulfilled the expectations of the hypothesis. He used two races of peas, in one of which the form of the seed was round, *A*, in the other angular, *a*. In the round seeds the albumen was yellow, *B*; in the angular seeds the albumen was green, *b*, thus —

AB, seed parent	*ab*, pollen parent
A, form round	*a*, form angular
B, albumen yellow	*b*, albumen green

The outcome of the experiment conformed to the scheme given above. It should be noted that in the first generation, *ABab*, the hybrid will contain all of the possibilities, although *A* dominates *a* and *B* dominates *b*. In the germ-cells the characters separate on the assumption of pure gametes, but in such a way that *A* will always be associated with *B* or *b*, *i.e.* the round form will always be yellow or green. Similarly, *a* will always be associated with *B* or *b*. Hence, as stated above, the only combinations possible will be —

AB, round and yellow,
Ab, round and green,
aB, angular and yellow,
ab, angular and green.

From the foregoing account it will be obvious that the problem will become more complex when three contrasted charac-

ters are involved. Mendel found that the results with three characters agree also with the expectations. As the number of characters increases further, the results will be very complex and difficult to detect except by an exhaustive series of experiments, although each single character can easily be traced and found to follow the Mendelian law. Under these circumstances we might anticipate that types differing in many characters would give results too complicated for analysis, especially if some of the characters follow Mendel's law and others follow other laws of inheritance. The generally accepted statement that species hybrids are intermediate in character between the parental types does not appear to hold in all cases critically examined for all the characters. It is evident that in the future the heredity of each character must be studied by itself.

Mendel's Law and the Germ-cells

On the assumption that the characters of the animal or plant are represented by primordia or elements or unit-characters in the chromosomes, the following attempt to account for the purity of the germ-cells, assumed on Mendel's hypothesis, has been suggested by Sutton.

In the early germ-cells, the spermatogonia and oögonia, the number of chromosomes is the same as the number in the body-cells, *i.e.* the somatic number; but just before the two maturation divisions there is a synapsis stage, in which the chromosomes come into closer connection with each other, and, as Montgomery has shown, it is probable that at this time the chromosomes pair with each other in such a way that each paternal chromosome unites with its homologous [1] maternal chromosome; and for the working out of Sutton's scheme it is essential that each paternal unites with its homologous maternal, *i.e.* that the paternal do not unite with any other maternal or with each other.

[1] Homologous chromosomes are those that have the same form, or, according to some writers, similar characters.

At one of the two maturation divisions the united pairs of chromosomes separate again and move into opposite cells (Figs. 1 and 1 *A*), so that one cell gets one and the other cell the other of each of the homologous chromosomes. Thus each cell will contain some paternal and some maternal chromosomes, but the number of the maternal may be different from the number

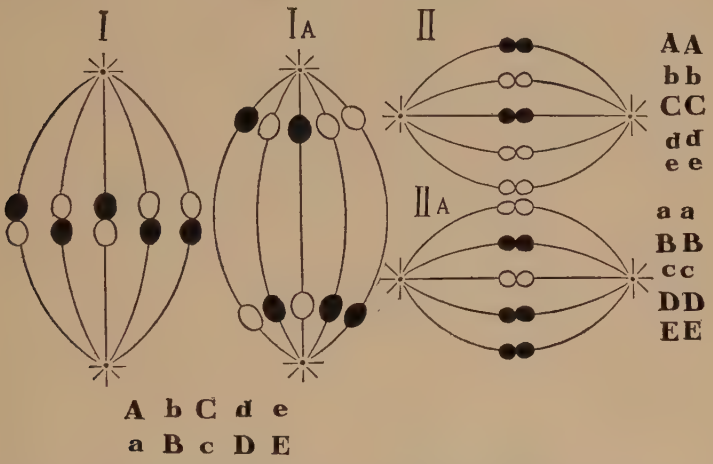


FIG. 6. Scheme to illustrate the two maturation divisions as seen in the spindle and chromosomes. The clear circles represent paternal chromosomes and the black dots the maternal chromosomes. In the first division, represented by I and I A, some of the maternal and some of the paternal chromosomes move toward each pole of the spindle. In the second division each paternal and each maternal chromosome divides into equal parts. In II the chromosomes of the cell derived from the upper end of I and I A is represented; in II A those from the lower end.

of the paternal. At the other maturation division[1] each chromosome divides equally Figs. II and II *A*, so that the daughter cells are exactly alike.[2] Thus there will be two cells of one kind in regard to the *single character* (or group of united characters) contained in each chromosome, and two cells of the other kind.

The same process occurs both in the egg and in the sperm-cells. In the egg three of the cells, the three polar bodies, are

[1] In some species the first, in others, the second, is the equation division.

[2] The *meaning* of this equation division has been much discussed, but nothing is known about it.

incapable of developing, and only the egg continues the history of the race. Half of the eggs, however, will on the average contain a particular kind of chromosome, and the other half the homologous kind, as shown in Figs II and II *A*.

It is of special importance to notice in this connection that the pairs of chromosomes are assumed to lie haphazard on the spindle, so that while in one pair the maternal chromosome may be turned toward a given pole, in another the paternal chromosome may be turned toward the same pole. In other words, there are no grounds for assuming that all the paternal chromosomes turn toward one pole, and all the maternal toward the other, but "accident" alone determines which way they come to lie on the spindle. Hence the possibility of various combinations of chromosomes in the different cells is given. The evidence in the favor of the assumption of the accidental position of the chromosomes is indirect, and is deduced from the way in which the characters appear in the offspring of Mendelian hybrids when more than a single character is taken into account. Without this assumption the chromosomal hypothesis given above will not apply for more than one character. Whether this assumption is entirely satisfactory, will be considered later.

A special case may make this discussion clearer. Let us assume that the character albinism of a white mouse is contained in *one* chromosome, and the gray character of the gray mouse in the homologous chromosome of the gray mouse. When these individuals are bred together the white chromosome, so to speak, and the gray chromosome are both present in the fertilized egg, which gives rise to the gray hybrid of the first generation, because the gray dominates the white. In the germ-cells of these gray hybrids the changes described above take place. At the synapsis stage the white chromosome pairs with the gray chromosome. Later, at one of the maturation divisions, the two separate and go to separate cells. Hence each germ-cell becomes "pure" and carries only one kind of color. If these hybrids (F_1) with white and with gray germ-cells are paired, there will be formed by chance unions of the germ-

cells the three kinds of individuals of the second generation. A white spermatozoön meeting a white egg, as one may say for brevity, produces a "pure" *recessive* individual; a gray spermatozoön meeting a gray egg gives a "pure" *dominant* individual; but when a white spermatozoön meets a gray egg, the offspring will be mixed, a heterozygote, and like the first hybrid (F_1).

If this hypothesis is true, we ought to be able to determine which groups of characters — where several are involved — are contained in a given chromosome, for the number of chromosomes is often small, and therefore the actual number of combinations is limited. All characters contained in the same chromosome should "Mendelize" together.

If we consider two characters, the principles stated above will apply. Let us take the case of the round and yellow, angular and green peas. The round form, A, may become combined with the yellow, B, or with the green color, b, giving AB or Ab; the angular form a with B or b, giving aB or ab. To work this out we must suppose the *color* to be contained in a different chromosome from the *form*, for otherwise they could not shift over. When the chromosomes unite in synapsis the A-bearing chromosome can only unite with a, and B can only unite with b. Hence since $\left\{ \begin{matrix} A \\ a \end{matrix} \right.$ and $\left\{ \begin{matrix} B \\ b \end{matrix} \right.$ may be turned either way on the spindle, A may pass into a cell with B or b, and also a into a cell with B or b.

Simple and logical as Mendel's assumption appears to be on the hypothesis of each character being contained in only one of the chromosomes, yet I do not think it can be accepted in this form because the primary assumption that each character is contained in a single chromosome and not in others is highly arbitrary, and also because there are certain actual results that are difficult to explain on the assumption of "pure" germ-cells. In fact, it has not been shown beyond question that the chromosomes are the bearers of the hereditary qualities. The evidence that is generally supposed to establish the assumption of

the hereditary nature of the chromosomes is that the spermatozoön brings into the egg only the chromosomes of the male germ-cells. While it is undoubtedly true that the largest part of the sperm-head is made up of chromatin material derived from the nucleus, it is also true that the protoplasm of the original germ-cell is not lost. It is partly used up in the formation of the tail of the spermatozoön, but also forms a condensed layer around the sperm-head. There is every reason to assume that the latter may become incorporated as a part of the cytoplasm of the egg. There is also another serious objection to the explanation of the purity of the germ-cells given above, for, even if the chromosomes be the bearers of the hereditary qualities of the egg and sperm, it does not follow that each unit character would be contained in only one chromosome. If it be assumed that each chromosome carries all the hereditary qualities, it is impossible to account for the purity of the germ-cells on this assumption. For instance, if we assume that each of the chromosomes contains all of the hereditary characters, the germ-cells of the hybrid, $A(B)$, will contain, before synapsis, half of their chromosomes bearing the character A, and half bearing the character B. If these unite at the synapsis in pairs, and then come to lie, haphazard, on the spindle, some turned one way, some the other, the resulting germ-cells will contain all mixtures of A and B, and hence be impure. If we give up the idea of "purity" and assume that the relative number of A or of B chromosomes determine the character of the resulting cells, the three types of the Mendelian ratio might be accounted for, provided the reduced number of the chromosomes is an odd number. If it were an even number, it must often happen that equal numbers of a character, of A or B, would be contained in the same germ-cell, and hence there would be an exact balance, which on the theory should give neither result. This, however, is not in harmony with the facts.

In the light of these theoretical difficulties it seems to me that the chromosomal theory must be applied to Mendel's law with caution, and that while at first sight it appears to offer an

explanation of the assumed purity of the germ-cells in the Mendelian cases, yet more careful consideration shows that in order to do so certain assumptions are necessary that are not above suspicion.

It may be seriously questioned, I think, whether the germ-cells of Mendelian hybrids are pure. It is true that the Mendelian proportion, 1 : 2 : 1, in the second (F_2) generation can be most easily accounted for by assuming two kinds of male and two kinds of female germ-cells, each kind existing in equal numbers; but the assumption that the two kinds must be *pure* germ-cells meets with serious difficulties when certain results are considered. It will suffice to point out here that the main difficulty lies in the behavior of the so-called extracted recessives which ought to be a pure strain on the assumption of "pure" germ-cells, but which have been shown on the contrary to contain in a latent condition the dominant character. I have tried to show that the results may still be accounted for even if the germ-cells of the hybrids of generation (F_1) are not pure in regard to any pair of contrasted characters, such as gray and white, but that both characters are present in all the germ-cells. The two kinds of germ-cells that the hypothesis calls for may be referred to the alternating dominance in the germ-cells of each of the two contrasting characters. The Mendelian proportion can be accounted for on this assumption as well as on the accepted interpretation of pure germ-cells, and the latency of the dominant character in the extracted recessive can also be explained on my view, but not on the other. An example may make my meaning clearer.

Suppose a white and a gray mouse are paired. The germ-cells of the white mouse are white-producing, or briefly white, those of the gray mouse are gray-producing, or briefly gray. The fertilized egg will contain both characters, and since the gray dominates the white, the symbol $G(W)$ will represent the condition in the mouse itself. In its germ-cells both the gray, G, and the white, W, exist, presumably combined in some way.

At some time in the history of these germ-cells one or the other of these two characters comes to dominate in each cell, so that half of the cells will be $G(W)$ and half $W(G)$. This will be true both for eggs and sperm. Chance meetings of the two kinds of sperm and the two kinds of eggs will give —

$$\begin{array}{cc} G(W) & W(G) \\ G(W) & W(G) \\ \hline 1\ G(W) + 2\ G(W)\ W(G) + 1\ W(G) \end{array}$$

This is the characteristic Mendelian proportion. The first term, $G(W)$, is a gray mouse, the so-called extracted dominant, *i.e.* it is a mouse gray in color, which, if bred to other gray extracted dominants, will produce only gray mice. This means that the latent white remains in the latent condition in its germ-cells, all of which are $G(W)$.

The second term, $G(W)\,W(G)$, of the proportion represents also a gray mouse, since the gray, G, dominates the white, W, when both occur in the "free" condition in the same body-cell. It will be noticed that the presence of the two "free" colors, G and W, in the cells of this type indicates that the type is the same as the first hybrid formed by crossing G with W; and it is important to find that when inbred this type gives exactly the same results (*i.e.* the Mendelian proportion again) as do the first hybrids, GW. By the "free" condition I mean to imply that the two characters, G and W, have not been brought into the intimate relation to each other that is assumed to occur in the germ-cells at the time when the alternating dominance and latency occurs.

The third term, $W(G)$, of the proportion is the extracted recessive. It represents a white mouse containing gray in a latent condition. If inbred, these white mice produce only white mice, but if crossed in certain ways the latent gray color can be brought out again.

The preceding example will suffice to show how the Mendelian proportion can be accounted for on the assumption of alternation of the contrasted characters in the germ-cells.

The question may be asked whether this method of accounting for the results can be referred to the changes that take place in the chromosomes of the germ-cells. The hypothesis demands that the contrasted characters come into relation with each other, and the union of the chromosomes might suggest such a possible combination. After uniting, the fused characters must be halved again (quantitatively not qualitatively), and the reduction division might suggest a possible method of accomplishing this result. On the other hand, there is no apparent need to assume such a complicated mechanism to bring about the union of the characters in the same cell, nor for their subsequent separation. Moreover, by referring the process to the chromosomes, we introduce the further assumption that the characters of the cell are contained only in those bodies — an assumption that is not itself established. For the present, therefore, it seems premature to connect these results definitely with any known change in the germ-cells, and the same statement holds also, as we have seen, for the alternative assumption of pure germ-cells.

Until we know more of the way in which characters are represented in the germ-cells, we can only offer purely speculative views of what we suppose might take place in order to give the Mendelian results. The formulæ that we use are merely symbols for handling these results. The fact that the characters that "Mendelize" are different types or permutations of the same characters suggests that they may represent stereometric relations of the material basis of the characters, *i.e.* of the molecules representing them. Thus we might represent the characters gray and white in the hybrids as right- and left-handed forms of the same molecule, and indicate this by *GW* and *WG*. Such germ-cells meeting each other would give —

$$\left\{\begin{matrix} GW \\ GW \end{matrix}\right. + \left\{\begin{matrix} GW \\ WG \end{matrix}\right. + \left\{\begin{matrix} WG, \\ WG \end{matrix}\right.$$

and these might be taken as representing the three Mendelian groups. Interesting as such a speculation might be, could we

find evidence in its support, it is unprofitable as an interpretation until or unless we can show that it is at least probable.

The preceding discussion is based on the idea that there must be two kinds of germ-cells in order to give the Mendelian results. This is perhaps the simplest way to formulate the problem, but it should not be overlooked that the results can also be explained by assuming that all the germ-cells of the hybrid are alike, containing both dominant and recessive characters, but that after fertilization internal or external factors determine whether the one or the other character dominates. The difficulty of this view is to account for the middle term of the Mendelian proportion, in which, although the dominant develops, the germ-cells seem to return to the two original kinds. Possibly this difficulty could be met by assuming that the two contrasted characters are so nearly balanced in half of the progeny, that while the dominating character dominates when differentiation begins, it is not able to do so in the germ-cells. It is evident, however, that this interpretation is more complicated than that of two kinds of germ-cells, and fails to account for the three sharply marked groups.

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CHAPTER VII

EXPERIMENTAL HYBRIDIZING (*Continued*)

Experiments with Mice

The ease with which mice can be kept in captivity, their rapid rate of multiplication, and the occurrence not only of an albino race, but of other fancy breeds as well, have made these animals a favorite subject for experimental work.

The house mouse (Mus musculus) is of a gray, sometimes called cinnamon or agouti, color. The white mouse is an albino race derived without much doubt directly from the wild form. Albino mice have been recorded as occurring in situations where there was no reason to suppose that their origin could be due to the escape of domesticated albinos. It is also known that in many groups of the animal kingdom albino individuals often suddenly appear.

The color of the hair of the gray mouse is due, according to Bateson and Durham, to three kinds of pigment often associated in each hair: (1) opaque black, (2) less opaque brown, (3) transparent yellow. In albinos all three colors have disappeared as well as the pigment in the eyes. As many as a dozen or more races of fancy mice are known. It appears that the color of the race is determined according to which of the three pigments found in the gray house mouse predominates or exists alone. Thus the golden agouti, of a tawny color, contains yellow and brown pigments, but not black; chocolate mice contain only the brown pigment; yellow contain only the yellow; black contain black and brown. Variegated mice are those in which irregular small spots of black or chocolate occur on a

white background; spotted or pied or piebald mice are those in which these various colors appear in splotches or marks. In addition to these kinds, a white mouse with dark eyes is known, which is probably — to judge from other white animals with black eyes — not derived from an albino, but from a spotted animal in which the spots of dark pigment have disappeared except in the eyes. The so-called dancing mice that whirl around at times are said to be of Japanese origin, and may have originated from a different wild variety.

Experiments on mice have been carried out by a number of investigators, the principal results being those of von Guaita, Cuénot, Parsons, Darbishire, Castle, Allen, Davenport, Schuster, Haacke, and others. Von Guaita's results were not considered by him in the light of the Mendelian ratio, but Bateson and Davenport have more recently examined them and have pointed out that many of them appear to follow Mendel's law.

Cuénot's results conform closely to the Mendelian law. He found that when a gray mouse is paired with an albino, the offspring in the first generation (F_1) are always gray mice — the gray dominating over albinism. The next generation (F_2) from the inbred dominant gray mice gave 198 gray and 72 albino mice, *i.e.* in the ratio of 2.75 : 1, a near approach to the expectation of 3 : 1. Later Cuénot reported that his "pure" gray[1] mice of the third filial generation (F_3) when crossed with albinos gave several *black mice.* These black mice when bred with certain albinos gave black mice, which appeared to be $B(W)$, *i.e.* black dominant, white recessive, for, when bred *inter se,* the offspring were three blacks to one albino. Some of these blacks were shown to be "pure" and produced a race of pure blacks. When individuals of this black strain were bred to ordinary gray mice, the *black was recessive,* giving in the second generation three grays to one black.

Cuénot made a further discovery of great interest. He found when he bred the black mice to albinos that the results were

[1] These were the offspring of the second generation that had bred true and shown themselves to be pure *G*'s.

different according to the kind of albinos that he used. For example, albinos that had been derived *through* a gray ancestor, *i.e.* the so-called extracted albinos, when bred with the black strain produced gray offspring. If, however, albinos that had been derived through a previous cross with a black mouse were bred with a black, the offspring were black. Again, albinos derived from a previous cross with a yellow gave either mixed yellow and gray, or mixed yellow and black. These results show that although albinos may all appear alike and breed perfectly true with each other, they belong in reality to different classes, whose latent characters are dependent on previous influences. Results of this sort are difficult to account for on the supposition that the germ-cells are pure. This property of latency is not something peculiar to albinos as certain published statements might have lead one to infer, but holds for the different colors also. A black race that breeds true may carry another latent color that can be brought out by crossing. Unless this fact is also taken into account the crosses with albinos may be misinterpreted.

Experiments with waltzing mice have been made by Haacke, von Guaita, and Darbishire. These mice are black, or white, or yellow and white; the mixed colors introducing a complication into the results, so far as color inheritance is concerned. As has been said, von Guaita's results with these mice were not considered from the point of view of Mendel's law, but Bateson, who has later analyzed the data, finds in some cases what seems to be an approximation to the expected proportions; in other cases this is not evident. A few of von Guaita's facts and their possible interpretations may be given. When the black-and-white waltzers were bred to ordinary albinos, the first offspring (F_1) were gray, like the house mouse, and of the same size, which is larger than that of the waltzing race. They also show the wild disposition. These mice (F_1) when inbred produced albinos and four colored types,—black, gray, black-and-white, and gray-and-white. There were 14 albinos and 30 colored individuals. The relation

of the colored types to each other as regards their inheritance is too obscure to make it profitable to discuss the result here.

Darbishire has carried out experiments with pink-eyed, spotted, waltzing mice crossed with albinos. In respect to their coat color, he recognizes six groups forming a continuous series, depending on the extent to which the pigment spots cover the surface of the mice. The colors of the spots were yellow, gray, black, lilac, or chocolate. When these mice were crossed with albinos, supposed to be pure, spotted mice were produced *with dark eyes*. None of the mice of this generation exhibited the waltzing habit. These hybrid mice (F_1) when bred *inter se* gave the following kinds of mice (F_2): —

Albino	137
Colored or piebald with dark eyes . . .	287
Colored or piebald with pink eyes . . .	131

Of these mice 97 showed the waltzing habit and 458 did not. The Mendelian expectation for waltzers is 138.75. The actual results fall considerably below the expectation, nevertheless it may be that some of the mice that did not waltz were potentially waltzers and might have transmitted this habit as do "pure" recessives. It is interesting to note that, whether the Mendelian proportion is or is not given, the waltzing habit disappears in the first generation of hybrids (F_1) and reappears in the second generation (F_2) as do other Mendelian characters.

The expectation for albinos is approximately realized as well as the expectation for the other two types. Since neither grandparent had dark eyes, this character must have been latent in one of them, because it appears in all of the offspring (F_1). Darbishire points out that his results do not conform in all respects to the Mendelian rule; but some, at least, of these difficulties are not insuperable, I think, if it be granted that the so-called "pure" recessives and "pure" dominants are really impure with latent characters that come out on crossing. Darbishire contends, and I think justly, that the behavior in inheritance of extracted

recessives and of extracted dominants cannot be accounted for, if they are supposed to have been formed by the union of *pure* germ-cells. On the contrary, he thinks that the results become intelligible only when the ancestry of these forms is taken into consideration. In other words, if "pure" recessives and "pure" dominants are really pure (as modern Mendelians have assumed), the ancestry of such forms could be ignored; but since the results are inexplicable on this assumption, the most reasonable conclusion is that the germ-cells are not pure. So far I am in agreement with Darbishire; but if this conclusion is meant to imply that the Galtonian assumption in regard to inheritance in these cases is the only alternative, I should dissent. I have tried to show how the Mendelian results may still apply without assuming that the gametes are pure, but by assuming that they show alternate dominance and latency.

Darbishire also crossed some of his first hybrids (F_1) with albinos and obtained 368 albinos and 378 dark-eyed piebald (or sometimes uniformly colored) mice. This gives a close approximation to the Mendelian expectation. He found, moreover, in this generation that the gap between the albinos and the least-colored individuals was greater than among the offspring of hybrids (F_1) when inbred. It is also interesting to note that with this cross the pigmented eyes appeared in all the piebald offspring. In other words, the latent color, eye-pigment, is maintained in the cross, since it dominates the pink-eyed type. Darbishire notes especially that these offspring (obtained from the hybrid and the albino) have more white in their immediate ancestry than have the offspring of the hybrids when inbred; yet the offspring show actually less white, and show more often the wild color and black (as compared with yellow and fawn color). The meaning of this he finds obscure, but possibly the results may be accounted for on the assumption of the latency of pigment in one or both parent types, which is brought out by crossing.

The subsequent history of the three classes of individuals obtained by inbreeding the first hybrids (F_1) is as follows: (1) The

extracted albinos give always albinos. Only 2 out of 94 waltzed. (2) The dark-eyed mice with colored coats belonging to the middle term of the Mendelian series should also give, if inbred, the three types again in the proportion of 1:2:1. In this connection Darbishire points out that on Galton's law of inheritance the farther the individuals of this middle class are removed from the first class, the fewer the albinos that should appear, since they are farther removed from the original ancestor that was white. On the Mendelian law the members of this middle term should always continue to give the same proportion, 1:2:1. Experiments that Darbishire made to test this point seemed to show that the results follow more nearly the expectation of Galton's law; but the purity of the types used may have seriously affected his results.

Especially interesting, it seems to me, are Darbishire's experiments with the extracted mice of the second generation having pink eyes and colored coats. If these are really pure, they should, if paired with pure albinos, produce animals similar to those of the parent cross between colored mice with pink eyes and albinos, *i.e.* there should be produced only spotted mice with dark eyes. This, however, was not the result obtained. Of 98 young, 12 were albinos, while one pink-eyed (colored) individual also appeared. These results are complicated by the fact that the albinos used were also the extracted offspring of hybrids paired with albinos. Nevertheless, even granting this, it offers no explanation of why albinos should appear, and the only explanation that seems reasonable is that the albino, latent in the pink-eyed mice, has affected the result, presumably being brought out again by crossing. Sixty-three of the 98 young were obtained from such contaminated albinos (extracted recessives). Only seven of the unions were between such pink-eyed mice and albinos which did not contain pink-eyed, spotted waltzers in their immediate ancestry. From these pairs 35 young were obtained, of which 10 were albinos — a relatively higher number of albinos, and approximately one fourth of the whole. The results seem to show that the extracted

"pure" race was not pure, since it may produce some albinos when paired with albinos.

Allen has also carried out a large number of experiments with mice. Crossing the gray house mouse with the albino gave gray offspring, as most other experimenters have found. The second generation (F_2) gave approximately the Mendelian ratio of three grays to one white, the former being partly pure grays, partly mixed. Crossing the dominant recessives (heterozygote) with the extracted albinos, where equality of grays and whites would be expected, gave 84 pigmented young and 64 whites. While there is only an approximation to equality here (74 of each expected), the deficiency in white may be due to insufficiency of numbers, but possibly to some other factor. Allen found that when spotted mice were bred to albinos the offspring were spotted, — often with *less* white than the original spotted parent, — and in some cases the white almost, or even completely, disappeared. Thus, although we may look upon the spotted condition as a unit-character that is dominant, its extent appears to be variable. In fact, a latent character may also come to light here that is not seen in either parent, but must be potential in one or in both of them. While the white parent might have been expected to add more white to the offspring, — on Galton's hypothesis, — the result is exactly the opposite.

When pigmented, heterozygote individuals (F_1) were inbred, they produced 159 pigmented young and 55 albinos (53.5 being the Mendelian expectation). In another experiment, pigmented, heterozygote individuals (F_1) were bred to pure albinos, giving 69 pigmented and 69 albinos, exactly the anticipated ratio.

Allen carried out a number of experiments made to test the inheritance of partial albinism, as he calls the condition when white areas are present along with colored areas. When "partial albinos" are bred to pure albinos, the young (F_1) were more nearly totally pigmented (as stated above), some showing no trace of white, others had white toes, or a white tip to the tail or even a few scattered white hairs. One only had a white spot

on the belly. Haacke and von Guaita found similar results. "The influence of the albinos in these cases seems to be to upset the condition of localization of the pigment, so that the pigment patches become more extensive, tending to cover the entire body surface, as in totally pigmented animals. In explanation of this observation it is suggested that the character total pigmentation may be transmitted by albinos, and when so transmitted dominates over the spotted condition." Cuénot has offered a suggestion to account for this possibility. The pigment is assumed to be due to the action of a ferment upon a chromogene substance. The albino may transmit the ferment but not the substance. The germ-cell of the black-and-white individual would then be assumed to convey the pigment, and, when to it more ferment is added by the white gamete, more pigment is produced in the offspring.

Cuénot has given a very clear and important analysis of his results with mice in his third contribution to "The Heredity of the Pigmentation in the Mouse." [1] He uses the letter *C* to denote any colored character, and *A* for the albino character; *G* for the color gray; *B* for the black; and *Y* for the yellow. Thus the wild gray mouse will be represented by *CG*, and the extracted albinos, having potentially the gray color, by *AG*. The black mouse will be represented by the formula *CB*; extracted albinos derived through black ancestors *AB*; the yellow mouse by *CY*; the extracted albino through yellow ancestors by *AY*.

When a germ-cell containing the character *CG* unites with one containing *CB*, the gray, *G*, dominates. When gray, *CG*, meets yellow, *CY*, the latter dominates. When *CB* meets *CY*, the yellow again dominates. When a colored germ-cell, *C*, meets an albino, *A*, the individual that develops has black eyes, but the color of the hair depends on which color accompanies *C* or *A*. As an example Cuénot gives this case: a black mouse, *CB*, crossed with an albino, *AY* (yellow latent), gives a dihybrid, *CBAY*. This hybrid has black eyes, because for

[1] Archiv. Zool. Expér. et Gén. 1904. Sér. 4, T. 2. Notes et Revue, p. xlv.

the eyes the color, *C*, always dominates; but the color of the hair is yellow, because yellow dominates over black.

The four types with which Cuénot has experimented give eighteen different combinations, which he shows by means of the following table: —

COLOR	HOMOZYGOTES OR PURE RACES	HETEROZYGOTES	
		MONOHYBRIDS	DIHYBRIDS
Gray	*CG* (wild)	*CGCB* *CGAG*	*CGAB*
Black	*CB*	*CBAB*	
Yellow	*CY*	*CYCG* *CYCB* *CYAY*	*CYAG* *CYAB*
Albinos	*AG* *AB* *AY*	*AGAB* *AGAY* *ABAY*	

Of these eighteen types there are six that are pure races,[1] *i.e.* they produce germ-cells that are all alike (homozygotes). Inbred, they give always the original types in all successive generations, and this holds also for the three albino types, having the latent characters gray, black, and yellow, *AG*, *AB*, and *AY*. The other twelve types are heterozygotes, resulting from the crossing of pure races. Of these, nine are monohybrids, having only one pair of antagonistic determinants; and three are dihybrids, having two pairs of antagonistic determinants.

It will be seen that Cuénot thinks that albinos are not necessarily all alike, although they may breed true to the albino type, but that they are different according to the latent character that each contains. The latent character may appear in

[1] According to Cuénot's nomenclature. The three albinos, homozygotes, belong in my opinion to a different category, for although they breed true, yet they contain a latent color that may come out in crossing.

some of the descendants, if these albinos are crossed with colored types. Thus if an albino *AG* be crossed with an albino *AB*, the albino offspring will be *AGAB*. Its germ-cells will separate into *AG* and *AB*, but these are albinos. If, on the other hand, a black mouse, *CB*, be mated with an albino *AY*, containing yellow as a latent character, the offspring will be *CBAY* (yellow), whose germ-cells will be of four kinds, *CB*, *AY*, *CY*, and *AB*. Crossing this yellow mouse (with its four kinds of germ-cells) with a white mouse, *AGAB*, obtained in the way just described, eight possible combinations may follow. The whole process is indicated in the following table: —

Parents	*AG* (albino) *AB* (albino)	*CB* (black) *AY* (yellow)
1st generation	*AGAB* (albino)	*CBAY* (yellow)
2d generation	*AGCB* gray (one)	
	ABCB black (one)	
	AGAY, *AGAB*, *ABAY*, *ABAB*	albinos (four)
	CYAG, *CYAB*	yellow (two)

Cuénot performed this experiment and obtained in the *second* generation 151 young, distributed as follows according to color: —

81 albinos, 34 yellow, 20 black, 16 gray.

The probability according to the formula $4n+2n+n+n$ is:

76 albinos, 38 yellow, 19 black, 19 gray.

The agreement is so close that there can be little doubt that the hypothesis is substantially correct.

Heredity of Piebald or Spotted Varieties. — The piebald condition is regarded by Cuénot as a special mutation, and not one due to crossing colored and white forms. *The piebald character appears in crossing to be dominated by the uniform coloration, whatever may be its tint.* For example, a spotted gray-and-white mouse crossed by a uniformly black mouse gives a uniformly colored gray mouse, showing that the coupled

114.600

characters, spotted *versus* color uniform, are independent of the coupled characters gray-black. Cuénot adds, therefore, a new character to the formula representing the uniform color, *U*, viz. its antagonist the spotted color, *S*.

From the point of view of heredity the spotted condition is peculiarly interesting, since it appears to be continually varying, and by suitable selection this spotted character may be carried through a regular progression until the dark color may almost disappear. The depigmentation begins at the tail, toes, and ventral surface of the body; more rarely there is a small spot on the top of the head. This is the condition found not infrequently in the wild gray mouse. Through selection the caudal and ventral white areas enlarge and the latter invades the flanks, right and left, finally meeting dorsally, producing a white girdle. The white invades the muzzle, then the head, where it may unite below with the ventral spot. Finally there remain two pigmented regions, both dorsal, one anterior and one posterior. The eyes always remain black. Cuénot is not sure that the development of the white may be carried so far that the black totally disappears from the hair, his experiments on these points not being sufficiently complete.

Cuénot studied the problems connected with the heredity of the spotted condition by making the following combinations: —

1. Cross between spotted and uniform coat.
2. Cross between a form much spotted (with white) and a form bearing the least possible amount.
3. Cross between two forms much spotted.

These experiments may now be considered in turn.

I. *Cross between Spotted and Uniform Coat.* — The couple uniform, *U*, and spotted-pigmented, *S*, follow rigorously the Mendelian rule of dominance with disjunction of the gametes. The spotted character is dominated in the first generation by uniform color. If a much-spotted mouse is crossed by one uniformly colored, the offspring that result show the dominant color without trace of spots. This result is all the more paradoxical, because if we cross a much-spotted mouse with an

albino, descended (extracted) from an animal with a uniform coat, one might be led to suppose that the white of the albino might go to augment the white of the spotted parent, but on the contrary these hybrids are uniformly colored. In the next generation the two characters, *U* and *S*, separate, *i.e.* disjunct, and the offspring give the Mendelian proportions $U+2US+S$, *i.e.* one spotted to three uniform.

II. *Cross between Two Forms unequally spotted with White.* — If a much-spotted individual is bred to one very little marked with white, having for example only a little white at the end of its tail, the offspring shows that the maximal dark marking is the dominating character. All the young have the tail partially white, but no other white marks on the body. Yet these young are not all exactly like the darker parent, since the degree of tail marking, for example, may be quite variable. In the next generation, when the young are inbred, the phenomenon of disjunction appears. Two groups of offspring arise, one oscillating around the least amount of white (one grandparent type), the other around the most white-spotted type (the other grandparent type).

III. *Cross between Two Much-spotted Forms.* — Without exception the young are spotted, but in variable degrees. The cross may even produce albinos if the two parents are hybrids, including the character *A*. These albinos, in turn, possess latent the spotted character.

Progression of the Spotted Condition by Selection. — Beginning with mice little marked with white and excluding in each generation the less-marked individuals, Cuénot found that the white areas could be increased slowly but regularly, so that in two and a half years mice were obtained that contained much white, and differed to a large extent from the first forms used. The details of the spotted type seem not to be represented in the germ-plasm, because the young and the parents are not identical. Local factors appear to determine the limits of variation.

In regard to the characters of albinos, it has been pointed out that they carry in a latent form the characters of the race from

which they have sprung.[1] If, for example, the characters spotted and uniform coloration be considered, the number of possible latent characters contained in albinos is given by Cuénot in the following table: —

HOMOZYGOTES OR PURE RACES	HETEROZYGOTES	
	MONOHYBRIDS	DIHYBRIDS
AGU	*AGUABU*	*AGUABS*
ABU	*AGUAYU*	*AGUAYS*
AYU	*ABUAYU*	*ABUAYS*
AGS	*AGSABS*	
ABS	*AGSAYS*	
AYS	*ABSAYS*	

All these forms "prove to exist" and may lead to diverse results when different albinos are bred. Only by hybridizing can the latent characters of the albino races be brought to light. Cuénot thinks that the results of a number of authors find their correct interpretation in the latent character in the albinos employed.

In a later communication Cuénot gives the results of some further experiments with gray, *G*; black, *B*; brown, *R*; and yellow, *Y*; and with the corresponding albinos, *AG*, *AB*, *AR*, and *AY*. A most remarkable result was found in the case of the behavior of the yellow race. It dominates all the other colors, yet when a yellow mouse is crossed, for instance, with a gray, half of the offspring only are yellow, the other half being gray, or black, or brown (according to the recessive colors present). In Mendelian terms this means that the yellow mouse never produces pure yellow gametes alone, but some yellow and some of another color (gray, black, or brown). The same result follows when white mice, having recessive yellow, are crossed with gray, black, or brown. There result not only yellow offspring, but the other colors as well. If the yellow is a

[1] Whether an *albino mutant* differs in this respect from an *extracted albino* cannot be stated. Cuénot appears to deal with both types, regardless of their origin.

heterozygote, it should give, when crossed with a pure race, half yellow and half the other color (as stated above), according to the formula: $CYCG \times CGCG = CYCG$ (yellow) + $CGCG$ (gray). The gray offspring should be pure and never produce any yellow. Such was found to be the case. Thus of 355 young there were 177 yellow and 178 gray or black. The gray or black do not include the recessive yellow — at least yellow mice never appear in their progeny.[1]

The remarkable fact, referred to above, is that it is impossible to obtain a pure yellow race, CY. Theoretically one would expect to obtain, Cuénot thinks, such a race by crossing two similar, heterozygote, yellow mice. Thus —

$$CYCG \times CYCG = \underset{3 \text{ yellow}}{CYCY + 2\ CGCY} \quad \underset{1 \text{ gray}}{CGCG}$$

One third of the yellows should be pure yellow with gametes all CY's. They should breed true to their color. Of 81 yellow mice obtained by such combinations, not one proved to be pure CY's. In connection with this result, Cuénot finds that there are always fewer yellows than expected on the last formula, which gives 75 per cent yellow to 25 per cent grays. If we assume that this is due to the absence of $CYCY$, then we should expect 66.6 per cent yellows to 33.3 per cent grays; but neither does this occur,[2] and the proportions are more nearly 75 per cent to 25 per cent. Therefore Cuénot offers the following explanation: Since his yellow mice were never homozygotes, it follows that the combination of CY with CY can never occur in fertilization, although Cuénot thinks that other results show that a disjunction of CY from the other colored characters takes place. This means that these gametes, CY, can never meet to give the zygotes having the formulæ $CYCY$,

[1] Nevertheless yellow must have been latent, as in the case of albinos that contain a latent color and still breed true.

[2] Professor E. B. Wilson has pointed out that even if the CY sperm never fertilizes the CY eggs, the expectation would still be 75 :: 25, because the CY eggs would be fertilized by other sperm.

AYAY, and *CYAY*. In other words, selective fertilization occurs.

It seems to me that this is improbable and that a simpler assumption may account for the results. Cuénot's yellow mice were obtained through an albino of unknown ancestry. He crossed them with gray (or with black) mice, and obtained *dominant yellow* mice, to which he assigns the formula *CYCG*. These when inbred should give, according to Cuénot, on the theory of disjunction of the gametes, *CY*- and *CG*-gametes. The offspring would then give the Mendelian proportion—

$$1\ CYCY + 2\ CYCG + 1\ CGCG.$$

But no mice represented by *CYCY* were obtained. It seems to me more probable from the results that the yellow does not separate from the other colors, and if so all the germ-cells would be on my view *CY*(*CG*) or (*CY*)*CG*. Such forms inbred would not give *CYCY*, as Cuénot assumes, but the dominant heterozygote *CY*(*CG*).

This point of view assumes that the yellow is so slightly prepotent in the extracted dominant, *CY*(*CG*), that the gray may dominate in half the germ-cells, giving *CY*(*CG*) and *CG*(*CY*). If this is true, gray mice would appear in one-fourth of the offspring of these dominants. The yellows differ on this point of view from all other extracted dominants in the failure of the yellow to remain dominant in the germ-cells.

Schuster has made a number of pairings between gray and white mice. Seventy of such families (F_1) were gray;[1] two families contained yellow mice and gray mice; one family contained four chinchilla mice only; and one contained two chinchillas and one gray. The appearance of these yellows in the first hybrids is ascribed by the author to the presence of yellow in the white parents,—the yellow dominating the gray of the first hybrids. Whether the same explanation will account for the chinchillas is not known, because the dominance of the chinchilla has not been tested.

[1] Containing 342 mice.

The gray (F_1) hybrids were paired with albinos and 537 young produced, of which 261 were albinos and 276 colored — a close approximation to the expected equality. The colors were of various kinds, but gray greatly predominated. When gray (F_1) hybrids were inbred, they produced 119 albinos and 308 colored — a rough approximation to the expectation of 1 to 3.

Haacke has published the results of a large number of crosses between white mice, colored mice, and Japanese waltzing mice. Although his experiments were not carried out to test the Mendelian law, yet, as the author points out, they closely conform to this law. Haacke states his general conclusion in a somewhat involved way, namely, that the possible races of species equal the number of possible kinds of germ-cells, *i.e.* equal a sum that consists of as many factors as a particular species has independently variable qualities or germinal portions. In the sum each factor equals the number of all possible modifications of its properties.

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CHAPTER VIII

EXPERIMENTS WITH OTHER MAMMALS AND WITH BIRDS

Experiments with Guinea Pigs

The hair of wild guinea pigs or cavies shows the same three pigments present in mice, viz. black, chocolate, and yellow. Domesticated cavies may show the following colors: the agouti cavy with the hair containing the black, yellow, and chocolate pigment. The yellow cavy with only yellow pigment. The red cavy is a dark, yellowish red. The chocolate cavy has chocolate pigment predominating. The black cavy has black pigment predominating over the other two. The albino cavy is principally white, although an entirely white individual seems never to occur; for pigment is generally found in the extremities of the body, on the feet, or nose, or ears, and sometimes in hairs on the body also.

In addition to these there occur spotted or pied races. Any one of the colors may be combined with white. A great variety of markings result in this way, since the pigment areas may be of different colors.

Brindled *cavies* have black and red hairs interposed in the same patches. Roan animals have white hairs interspersed with red ones. Silvered cavies have black and white hairs.

Castle has carried out through several years experiments with differently colored and marked races of these animals.

Crossing Uniformly Colored Types. — The self-colored races, as well as the albinos, breed true: thus Castle found albinos bred *inter se* gave 156 young, all albinos; pure pigmented individuals gave 261 young, all pigmented. On the other hand, albinos mated to pigmented animals gave in the first generation

314 young, all pigmented; and these last give in later generations some albinos. The results agree fairly closely with Mendelian expectations.

Castle has found, as had Allen and Cuénot for mice, that albinos, although breeding true, may carry latent or suppressed

FIG. 7. Upper figure, short-haired, smooth coat red guinea pig. Lower figure, long-haired, rough coat albino. (After Castle.)

colored characters. Thus one albino individual, a male, when mated with red females produced offspring marked with black. Another albino crossed with the same and with other red females gave young marked with black and red in about half the cases, the other half showing only red or yellow, but no black. A third albino mated with red females produces only red or yellow offspring, never black ones. In the light of these results, Castle

makes a distinction between recessive and latent characters. Recessive characters are those that disappear in the Mendelian sense when brought into contact with a dominant character. This recessive character is transmitted distinct from the dominant character in half the gametes of the hybrid. A latent character is a "condition of inactivity in which a normally dominant character may exist in a recessive individual or gamete." This latter is illustrated by the latent pigment carried by extracted albinos. Cross-breeding is necessary to bring the latent character to activity again.

When elementary pigmented types, or so-called pure races, of different colors are crossed, neither color dominates perfectly in the offspring. For example, when a black individual is mated with a red one, the offspring are blackish, but not so black as the black parent, red being also present, although masked somewhat by the black. The agouti type carries the three pigments black, chocolate, and red-yellow. When crossed with pure black it gave in one case one agouti and two black individuals.

Agouti crossed with red gave four young, three of them agouti spotted with red, one red spotted with agouti and white. Black animals seem to contain always some red pigment, which may appear when crossed with albinos. Red animals may, however, be free from black. Red crossed with white gives results that depend on the latent pigment characters borne by the albino, so that black offspring may appear among the others. A case of special interest is found in white animals with black eyes, which are therefore not albinos.[1] *They do not seem to be albinos but may contain recessive albinism.* They arose from spotted ancestors, and Castle regards them as spotted animals themselves with the pigment spots obliterated except in the eyes. These animals bred *inter se* or with albinos produce offspring with colored patches of greater or less extent. Whether by selection the white animals with black eyes could be made into a fixed race remains to be shown, and judging from what breeders of

[1] Two such animals appeared in Castle's experiments.

cattle have been able to do it seems not improbable that this might be accomplished.

Castle draws attention to the curious point that red and yellow cavies, having no black pigment in their coats, do not transmit black coat-pigment to their offspring, although they do transmit black eye-pigment. It would be erroneous, he thinks, to conclude from this that the eye-pigment is something altogether different in its inheritance from coat color, because when mice with coat patches but devoid of eye-pigment are mated with albinos, the offspring have pigmented eyes — a character that neither parent possessed

Heredity of the Rough Coat. — Some races of domesticated guinea pigs show the hair arranged in whirls or rosettes. When best developed the rosettes are found around the following *paired centers:* (1) the eye, (2) a point immediately behind the ear, (3) the shoulder, (4) a point dorso-lateral on the body, (5) the hip, (6) the groin, (7) each of the single pair of mammæ; and from two *unpaired centers*, viz. (8) the middle of the forehead, and (9) the navel. The direction of the hair is also reversed on the toes.

These rough-coated individuals breed true. When crossed with smooth-haired individuals the rough character dominates. The rough character of the offspring is *usually* as fully developed as in the rough parent. However, certain smooth individuals when crossed bring about a weakened condition of the rough character, some of the rosettes being less developed or even absent. These partially rough individuals may transmit to their descendants the fully rough condition. The result is important in that it shows that what we must regard as a new character in the species, viz. a rough coat, dominates when a back cross is made.[1] On the other hand, Castle has also found that repeated crossing of rough individuals with *prepotent* smooth ones results in further weakening of the rough character until it is almost eliminated — one after another of the rosettes disappearing. The weakening does not follow a definite decline, but

[1] See Castle's analysis, pp. 47–50.

in some cases may be slow, in others sudden, so that the intermediate steps are passed over at once.

Heredity of the Long Coat. — A race of long-haired cavies is known, either smooth (Angoras) or rough (Peruvians). The two sets of characters, long *versus* short, and smooth *versus*

FIG. 8. Upper figure, long haired, smooth coat albino guinea pig. Lower figure, short-haired, rough coat, black-red pigmented guinea pig. (After Castle.)

rough, are independent of each other in their behavior in heredity. The long-haired is recessive in relation to the short-haired or ordinary types. The long hair is not present at birth. The coat of the short-haired guinea pigs reaches its maximum length (about 4 cm.) not far from the age of one month, and is then gradually shed and renewed. On the other hand, the hair of the long-coated animals is apparently not shed at this period, but

keeps on growing. At three months it is 6 to 9 cm. long. If shedding now takes place the animal never acquires longer hair; but animals that reach the age of four months without shedding their longest hairs may ultimately acquire hair 14 to 16 cm. long.

It has been stated that long hair is recessive to short hair. When two long-haired individuals are mated, having hair of different lengths, the offspring have hair like that of the shorter-haired individual. In the next generation both long- and short-haired individuals occur, but the number of long-coated individuals exceeds the Mendelian expectation.

A pure albino, long-haired, and rough-coated individual, was crossed with nine different pure, pigmented, short-haired, and smooth females. Twenty-nine young were produced, all pigmented, short-haired, and rough-coated. Thus while two of the dominant characters come from the smooth-haired father, the third comes from the rough mother — the rough coat dissociating from the long hair to influence the arrangement of the short hair of the progeny.

Castle and Forbes have recently extended Castle's earlier experiments with short- and long-haired guinea pigs. When crossed the short hair dominates, but the hair of the hybrid is nearer the upper limit of variation of the pure, short-haired type, showing perhaps the influence of the other character. When the hybrids were inbred not only the two grandparental types reappeared, but a new intermediate type was present. This type contained individuals of all intermediate grades between the long- and short-haired types. It contained, first, individuals whose hair grew continuously from the age of twenty days on, but much more slowly than does the long hair, and shows a tendency to break off at lengths much less than that of the long hair. The long hairs were less numerous, as if some of the hairs only were continuous in growth, while the other hairs ceased to grow after a time. The alternative characters behaved somewhat like a mosaic. In other individuals the hair ceased to grow, *i.e.* was determinate in growth, but not until it had reached a length of 60 to 80 mm. These cases seemed to be a blend, but no

sharp line existed between the blend and the mosaic condition. In all there were 29 short-haired, 12 intermediate, and 10 long-haired individuals. The Mendelian expectation for these 51 individuals would be 38 short-haired and 13 long-haired. Thus there are fewer long-haired and fewer short-haired individuals, and the presumption is that each kind has contributed to the intermediate group.

When a long-haired individual was mated with a short-haired dominant-recessive (which gives in other Mendelian cases equal numbers of dominant-recessives and recessives) there were produced 14 short-haired, 17 intermediate, and 19 long-haired offspring. The results seemed to show that many of the germ-cells of the dominant-recessive had intermediate characters, and were not segregated into the two groups of pure Mendelian gametes. The authors conclude that the intermediate group is probably a new hybrid combination, and that its germ-cells do not split up into long- and short-haired types.

A few other experiments were also carried out that seemed to show that cross-breeding produces a "contamination of the gametes." Instead of pure types separating in the germ-cells of the hybrids, some mixing occurs. Another cross increases the amount of contamination, or at least it produces a larger number of intermediate forms. The authors appear to look upon the "contamination" as a partial or incomplete separation of the characters in the germ-cells of the hybrid. The evidence may be equally well interpreted, I think, to mean that the results are due to incomplete dominance of the dominant character. In other words, it seems to me that these results may be more easily "explained" on my interpretation of the behavior of the gametes in Mendelian cases than in the "modified" Mendelian explanation of the authors.

Castle and Forbes found in a family of short-haired guinea pigs a few individuals with hair about twice as long as that of their parents. Mated together they produced all long-haired offspring of the same kind. By selecting the best long-haired individuals for two generations a race of imperfectly long-haired

guinea pigs was produced, which compared favorably with the intermediate groups described above. Crossed with long-haired individuals two kinds of offspring were produced, with long and intermediate hair, but with no definite line of separation.

Experiments with Rabbits

Hurst has carried out a series of experiments with rabbits that have given results of unusual interest, especially in connection with the inheritance of color and of length of hair. Two races that were known to breed true were used, namely, white Angoras and Belgian hares. The former is an albino breed with pink eyes and silky hair. These animals have a peculiar habit of swaying the head when at rest. The Belgian hare has a pigmented skin, dark eyes, and short yellow-gray fur. When crossed the hybrids were pigmented like the Belgian hares, but the hair had lost the yellow color and was gray, like that of the common wild rabbit. When these first hybrids were inbred they produced 14 distinct types in the second generation, viz.: —

1. Hair short, pigmented, gray, uniformly colored.
2. Hair short, pigmented, gray, marked.
3. Hair short, pigmented, gray, Dutch marked.
4. Hair short, pigmented, black, uniform.
5. Hair short, pigmented, black, marked.
6. Hair short, pigmented, black, Dutch marked.
7. Hair short, albino, white.
8. Angora, pigmented, gray, uniform.
9. Angora, pigmented, gray, marked.
10. Angora, pigmented, gray, Dutch marked.
11. Angora, pigmented, black, uniform.
12. Angora, pigmented, black, marked.
13. Angora, pigmented, black, Dutch marked.
14. Angora, albino, white.

This "epidemic of variation" in the second generation of hybrids has been the common experience of experimenters both in animals and plants, and before the Mendelian principles became

known remained practically unexplained. By the aid of the Mendelian principles we are able to see at once that there are at least four pairs of distinct characters concerned in the offspring of the second generation, each pair being inherited independently of the other; namely, short hair *versus* long hair, pigmented coat *versus* albino, gray *versus* black coat, uniform *versus* marked coat.[1] Hurst takes up these four pairs of contrasting characters and deals with them separately.

Short Hair versus *Long Hair.*—The short hair of the Belgian breed rarely exceeds one inch, while the long hair of the Angora breed may exceed six inches. The first hybrids had short hair, the influence of the Angora not being apparent. A careful examination, however, revealed what appeared to be faint traces of the Angora influence in both length and texture. The hairs of the hybrid coat were slightly longer, seemed softer to the touch, and were apparently more densely distributed than in the pure short coat. These traces of Angora influence are slight and might easily be overlooked.

When these short-coated hybrids (F_1) were inbred, there were produced 171 young, of which 70 reached the age of two months or more, when the character of the hair becomes manifest. Of these 53 were short- and 17 long-haired. This is a close approximation to the Mendelian expectation of 51 to 17. The short hair was like that of the grandparent, the long hair like that of the other grandparent. When the long-haired Angoras were bred together they produced in the next generation only Angoras. The short-coated individuals mated together gave both short-haired and Angoras in Mendelian proportions.

Pigmented Coat versus *Albino.*—The cross gave in one case 26 totally pigmented individuals; in another case the fore-feet showed some white markings, which Hurst thinks is not due to the albino influence, but to Dutch marking latent in the albinos. The hybrids, when inbred, produced 132 pigmented and 39 albinos, the Mendelian expectation being 129 : 43.

[1] In the marked coat there is white on the ends of the feet and the tip of the nose. The Dutch is an extreme form of this marking.

The albinos subsequently bred true; the pigmented types were of two kinds, — pure and hybrid.

Gray versus *Black.* — When the yellow-gray Belgians were mated to the white Angoras, wild gray hybrids were produced. These, as stated above, when inbred, gave both colored and white offspring in Mendelian proportion, but some of the colored individuals were black instead of gray. There were 85 grays to 25 blacks. The grays, as stated, were like the wild gray instead of the yellow gray of one grandparent, although a few appeared to contain somewhat more yellow than the wild type. The blacks had no gray, but it is interesting to note that after the first molt a few white hairs appeared, which increased in number with each molt until some of the individuals resembled the silver-gray breeds (chinchilla). The blacks when inbred produced only blacks, the grays were of two kinds, — pure and hybrid.

"The sudden appearance of the black character in the second generation was quite unexpected as there had been no black individuals in the ancestry of either of the original parents . . . for at least eight generations, and probably many more. The fact that these black individuals appeared in about the proportion of one quarter, and bred true at once, was very significant from the Mendelian point of view. It suggested that the hybrid grays of the first generation were giving off gametes, one half of which contained the factor for black coat color. That it was not introduced by both is clear from the absence of black in the first generation." It could not have been introduced with the Belgians because these mated to black gave only grays. The black must, therefore, have been introduced with the albinos. Hurst carried out some further experiments that seemed to substantiate this view. One male, albino Angora mated with four black does produced 16 black young; but another albino female mated with black produced 5 black and 6 gray young. Hurst interprets these results to mean that the first albino gave off gametes that all carried black, while the second albino gave off gametes some of which carried black, others gray. When the white male and the white female used in these experiments were mated, only

white offspring were produced; but when one of these offspring was mated with a pure black, 5 blacks and 1 gray were produced. The albino must have carried, therefore, both gray and black.

Uniform versus *Marked Coat.* — It was found that the uniform coat of the Belgians breeds true, but mated with albinos gave, in two cases, somewhat different results: in one case the offspring showed no trace of markings (white); in the other case 15 of the young were marked with more or less white on the forefeet, shoulders, breast, nose, and forehead.

The subsequent history of these two sets of offspring was as follows: (*a*) Three of the uniform or self-colored individuals were bred together and with a pure self-colored individual, producing 35 self-colored and 2 slightly marked individuals having a few white hairs on the tip of the right paw. The third generation of the uniform individuals gave only uniform offspring. (*b*) Four of the marked individuals produced 67 young, of which 16 were uniform, 34 were slightly marked, and 17 had the maximum of white (Dutch markings). In the third generation three of the uniform individuals produced 14 uniform and 1 slightly marked. Also in the third generation the Dutch marked produced 10 young, all Dutch; and three of the marked individuals produced 3 uniform, 12 marked, and 2 Dutch. Hurst interprets these results to mean that one of the Angoras, although of pure stock, contained Dutch markings, latent, and when crossed these appeared. When these gametes united with the pure uniform gamete the slightly marked individuals of the first generation were produced. Afterward segregation of the gametes occurred, so that subsequently gametes for uniform and for Dutch markings appeared in about equal numbers with the result that in the second generation there were one quarter pure uniform, one half hybrid marked, and one quarter pure Dutch. It is interesting to note that this analysis leads to the conclusion hat "the coat-pattern characters — unlike the previous characters dealt with — are neither dominant nor recessive toward one another, but when crossed give intermediate hybrids in the first generation. In the second and third gen-

erations, however, these characters appear to follow the ordinary Mendelian rules of segregation and gametic purity." Hurst calls attention to the similarity of these results to those of Cuénot with spotted mice. The results are in agreement as far as the marked coat is a unit-character following Mendelian lines, and in so far as it may be carried by albinos in a latent state. The two results differ in that the marked coat in mice is completely recessive to uniform coat, while the Dutch markings in rabbits are neither dominant nor recessive at first, but give variable hybrids.

Castle has made a few experiments with rabbits, but the results gave little that was new in principle. "A cross between two different types of albino rabbits, Himalayan and pure white, shows imperfect dominance of the Himalayan character in the offspring, but complete segregation among their gametes." Long-haired rabbits bred to short-haired individuals give offspring with short hair. When rabbits with ears of different length are mated, the offspring have ears intermediate in length. In this character, blending appears to take place, and neither dominance nor segregation.

Experiments with Rats

Rats have been used much less than mice, and the results seem to be more complicated. Crampe has published the results of a large number of experiments, extending over ten years; but as the experiments were made before the importance of Mendel's theory was appreciated, it is difficult to interpret from this point of view the data obtained. No more striking instance could be given of the insight into cross-breeding experiments furnished by Mendel's law than a comparison of the work before and after this period. Confused and irregular as the earlier results appear, they arrange themselves into orderly groups in the light of this law. It is, of course, difficult now to show in all cases that Mendel's law unravels Crampe's results, since the records are often incomplete on important points, where further tests are requisite to interpret the result. Nevertheless Bateson's analysis of Crampe's data indicates that the outcome shows in many

cases the Mendelian expectation. Crampe found that when wild gray rats, *Mus decumanus*, were bred to albinos, the offspring (F_1) were of two kinds, viz. either (I) gray like the wild rat, or (II) gray with white marks. If the former (I) were bred *inter se*, the following types appeared: —

1. Self-gray.
2. Gray with white marks.
3. White and gray.
4. White (albino).
5. Black-and-white.
6. Black with white marks.
7. Black without marks.

If the other group of offspring (II) was used, *i.e.* inbred, all of the preceding types except 3 (white and gray) and 5 (black-and-white) were produced.

Bateson states that the great variety of types that appear here is difficult to interpret, but that such occurrences are by no means uncommon. He suggests that two classes of germ-cells may be present either in the albinos or in the wild gray rat.

The albino is recessive to all the other six types, as shown by crossing these with albinos. The extracted albinos bred *inter se*, whatever their origin, gave only albinos. In this connection Crampe makes another statement of interest. Albinos that had been bred true for several generations behaved differently from extracted albinos. The *former* albinos were simply recessive on being crossed with colored rats, while the *extracted* albinos gave a mixture of ancestral types when crossed with colored types. The result appears to be similar to Cuénot's with mice where the ancestry of the albino appears as a factor in the product.

On breeding *inter se* each of the seven types given above (F_1), Crampe found that the offspring (F_2) belonged to the following types: —

Type 1 might give types	1	2		4		6	7
Type 2 might give types	1	2	3	4	5	6	7

Type 3 might give types	3	4	5		
Type 4 might give types		4			
Type 5 might give types		4	5		
Type 6 might give types		4	5	6	7
Type 7 might give types		4		6	7

Thus the wild type 1 is dominant to all the others, *i.e.* its offspring may belong to any one of the other types which must have been recessive in its germ-cells. The gray forms 1, 2, 3, are also dominant, in the same sense, to the black forms. The albinos give albinos only. "It appears that types 3 and 5 could be ultimately bred true. As to 6 and 7, the evidence is not very clear; but as I understand the account, neither was completely freed from throwing the other. The breeding in these types was the least successful and extensive. Possibly they are illustrations of the Mittel-rassen of de Vries. It is especially noteworthy that the gray-and-white type 3 and the black-and-white type 5 do not give rise to self-gray gametes or to self-black gametes, a fact found again in mice. We see, therefore, that there are gametes for black-and-white and for gray-and-white, each of which may behave as a single character and dominate over albino." [1]

When pure black-and-white rats were crossed with the wild gray rats, all the colored types might appear in generation (F_2) except albinos. In other words, the black-and-white do not separate, they are not resolved in the germ-cells, as other experiments also indicate. Crampe found further that black-and-white individuals that gave albinos in the first generation when bred *inter se* also gave albinos when bred to albinos. In this case the black-and-white individuals had probably arisen from a cross between black-and-white and albino, so that the albino (*and not the white of the black-and-white*) gave the white mice just mentioned. On the other hand, Crampe found that when the black-and-white rats did not themselves throw albinos, they did not do so in the first generation when bred to albinos.

[1] Bateson, Proc. Zoöl. Soc.

In the light of this analysis that Bateson has made of Crampe's data, there can be little doubt that Mendel's law applies to many at least of the phenomena of heredity in rats. This is made highly probable by the recent results of Doncaster. He finds that there are only two color types, brown (or gray) and black, and only two color patterns in the colored-and-white individuals. In addition there are albinos, but these may carry in a latent condition either the uniform black or brown color, or the piebald markings. Crosses between the black or the brown wild rat with the albino may bring out the latent characters of the albinos. Doncaster points out that Crampe's work shows that brown (gray) dominates black, and both brown and black dominate white. The self or uniformly colored races 1, 2, 6, 7 (and those having small white areas below) dominate the piebald condition 3 and 5.

Doncaster states that Crampe's brown forms 1, 2, 3, correspond exactly with the similar black forms 7, 6, 5, "but are less simple to work with since they may contain recessive black." He finds two varieties of type 6, — one with much white and one with very little. The latter belongs, in his opinion, to the uniform type. Crampe failed to make this deduction, so that one of his forms was probably heterozygous. Evidence that the inheritance in rats is Mendelian was found by Doncaster in a number of the crosses made to test this question.

Experiments with Cats

Doncaster has brought together a number of records, obtained from owners of pedigree cats, that show the color inheritance of certain breeds. He examined more especially the question as to why tortoiseshell cats are nearly always females. His conclusions, as will be seen, have an important bearing on the problem of dominance in relation to sex. Tortoiseshell kittens may be obtained in any of the following matings: —

(*a*) Tortoiseshell ♀ by tortoiseshell ♂
(*b*) Tortoiseshell ♀ by black or blue ♂

(*c*) Tortoiseshell ♀ by orange ♂
(*d*) Orange ♀ by orange ♂
(*e*) Orange ♀ by black or blue ♂
(*f*) Black or blue ♀ by orange ♂

In all of these matings, in addition to tortoiseshell, kittens of other colors may appear, viz.: —

(*a*) Tortoiseshell ♀ by tortoiseshell ♂ gives tort., orange, black.

(*b*) Tortoiseshell ♀ by black or blue ♂ gives tort. ♀, orange ♂, black ♂, ♀.

(*c*) Tortoiseshell ♀ by orange ♂ gives tort., orange, black.

(*d*) Orange ♀ by orange ♂ gives *either* tort., orange (or blue) *or* only orange.

(*e*) Orange ♀ by black ♂ gives tort., ♀, orange ♂.

(*f*) Black ♀ by orange ♂ gives tort., black (and probably orange).

(*g*) Black ♀ by black ♂ gives only black (or blue).

From these results it appears that tortoiseshell is a heterozygous color produced by the meeting of orange and black gametes. The explanation that tortoiseshell cats are nearly always females and rarely males is owing to orange nearly always dominating in the male over black, while in the female the dominance of the orange is incomplete, so that tortoiseshell results. In other words, in the female sex the orange and the black both exist together, while in the male sex the yellow usually dominates. A few examples will make the conclusion clearer. For instance, in mating (*e*) when an orange female is crossed with a black male, only tortoiseshell and orange kittens are produced; if both the orange and the black breeds are "pure," the female offspring are tortoiseshell and the males yellow. In the reverse mating (*f*), where a black female is crossed with a male orange, the male may be heterozygous (*i.e.* having both black and orange germ-cells), hence black kittens may also be produced. The kittens will be black males or females, tortoiseshell females, and orange males.

When a tortoiseshell female is mated with a black male, the male offspring will be orange, because the tortoiseshell is hetero-

zygous. It is also evident why orange females are very rare, although orange males are common, since in all matings in which one of the parents is black, orange can appear only in the male offspring. "If, therefore, the great majority of orange males contain recessive black, when they are paired with tortoiseshells, only a quarter of the kittens will be pure orange, and only half of these females."

The preceding statements show the relation of the colors orange and black. The inheritance of two other colors was also examined; namely, cream and blue. Cream appears to be a dilute form of orange, and blue of black. The blues breed true (when derived from yellow ancestors) and are therefore recessives or homozygous. A cream female and a blue male give blue tortoiseshell (blue and cream), cream males, but no blues, since the cream dominates incompletely in the female, completely in the males. On the other hand, a blue female and a cream male give blue tortoiseshell females, blues of both sexes, and possibly cream males. These and other results show that the dilute forms behave in the same way as do the stronger colors. Thus cream is dominant over blue in the male, but when blue and cream meet in the female a tortoiseshell results.

It has been stated that male tortoiseshell cats are known, although they are rare. It must be assumed that in such cases the dominance of the yellow is incomplete as in the female. This means that while complete dominance is usually associated with the male character, it is not necessarily always associated with this sex. It is interesting to find that when a male tortoiseshell is mated with a female of the same color, the kittens are tortoiseshell, orange, and black. This is what is expected on the assumption that the germ-cells of the tortoiseshell are black and orange (with the alternate character latent on my view). The prepotency of different tortoiseshell individuals (males) seems, however, to vary.

It should also be pointed out that the colors described above may be associated with a certain amount of white which reappears in the offspring without, however, affecting the inheritance

of the other colors. The piebald character stands as a unit contrasted with uniform coat, but is independent of any particular color.

Data for Other Mammals and Man

A few other cases in mammals, that seem to show discontinuous inheritance, are known. Castle and Davenport have both called attention to cases of so-called wonder-horses, *i.e.* horses with remarkably long mane and tail. In the case of "Linus I" the mane was 18 feet long and the tail 21 feet. The parents and grandparents of these horses also had unusually long hair, which increased in successive generations. The data are insufficient to show the relation of dominance and recessiveness in this case, but the persistence of the long hair seems to indicate its dominance.[1]

Harper and Hurst have recently examined certain data in regard to the inheritance of coat color in horses. Harper deals with the problem from the standpoint of prepotency of certain colors in regard to ancestry, selection, age, and sex. Hurst shows that bay and brown colors dominate completely chestnut, and there are definite indications that these two colors follow Mendel's law.

Some statistics recently published (1904) by A. G. Bell have furnished Davenport with material to study the relation of black color to white color in sheep. The data show that when three white individuals having as far as known white ancestors were crossed with black sheep, the 13 lambs resulting (F_1) were white, showing the dominance of white. Of 20 offspring from black parents all were black.[2] When a black (recessive) individual was mated with a dominant white (one of whose parents was white and one black), 26 lambs were white and 25 black, which is the Mendelian expectation. When a dominant-recessive white was mated to a dominant-recessive white, 40 were white and 7 were black. The expectation is 25 per cent black. The

[1] In guinea pigs the long hair is recessive.

[2] One uncertain case of white is given that is not above suspicion.

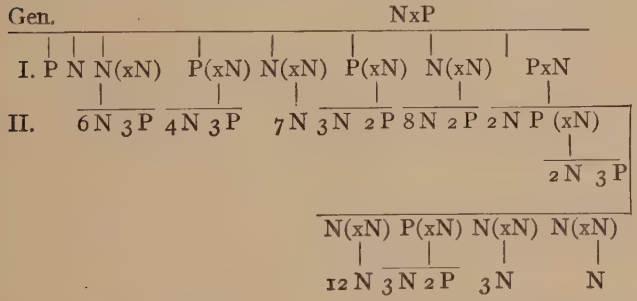
number of black lambs is too small on the assumption that chance meeting of equipotent "pure" germ-cells brings about the results.

Poulton [1] has given some records of polydactyl cats that appear to be explicable, so far as they go, along Mendelian lines. Three young were produced from a polydactyl female by an unknown father. They were all polydactyl. If polydactylism dominates over the normal condition, this result is simple dominance. One of these individuals (F_1) produced three litters (by unknown fathers), in which four normal and six abnormal kittens appeared. If the father was normal, five normal and five polydactyl young would be expected. Thus: —

$$\begin{array}{r} P + N \\ N + N \\ \hline 2\,NP + 2\,NN \end{array}$$

Only two kinds of discontinuous inheritance that may possibly follow Mendel's law have been shown for man. Albinism, according to certain data collated by Castle, may perhaps follow this rule. The cases referred to were albino negroes. Albinism is, of course, different in this respect from white. In the latter case, blending of the black and white occurs to produce mulattoes.

The other case is that of polydactylism. Fachenheim has given some statistics,[2] that Davenport has examined from the point of view of Mendelism. The accompanying table gives the inheritance through three generations: —

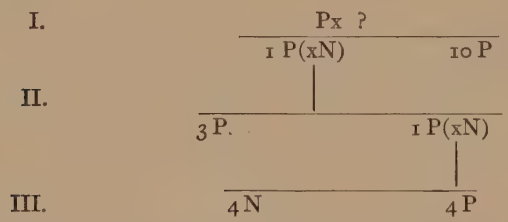


[1] *Nature*, 1883.

[2] Jena Zeitschrift, XXII, 1888.

If polydactylism is dominant and the normal condition is recessive, the chances are that any polydactyl person has had one normal parent and the germ-cells are therefore P and N.[1] Paired with a normal individual (N + N), half the children should be polydactyl and half normal. In the above case there were in fact in the first generation four normal and four polydactyl children. In the second generation when normal offspring paired with normal, 5 polydactyl children and 21 normal were produced; and when the polydactyl descendants paired with normal, 7 polydactyl children and 12 normal were produced. For the small number recorded, the latter result is not very different from 1 : 1, the Mendelian ratio. Again in the third generation when P was mated to N, 5 normal and 5 polydactyl children were born.

Struthers gives the following case of polydactyl inheritance in man: —



The result can only be explained on the Mendelian view by assuming that both parents of the first generation were polydactyls, *i.e.* produced germ-cells bearing polydactylism. It is necessary to make this assumption in order to account for the second generation that descended from one of the first filial generation. Here a polydactyl parent married a normal individual and produced only polydactyl children, showing that no normal germ-cells were present in one parent. Had there been some normal germ-cells, some normal children would be expected, provided the numbers are really large enough to give this result a chance to appear. In the third generation an equal number of the two kinds of offspring are expected, and such are found. A third case is

[1] Or P(N) and N(P) on my view.

given by Struthers.[1] A normal man married a woman who had six fingers on the left hand. There were 18 children, only one of whom was abnormal. In this case the polydactylism was not dominant except in one case; but among the normal children in the third generation one polydactyl individual is recorded, indicating that polydactylism was in the strain. The failure of the polydactyl condition to dominate in this case, except in one instance, shows how unsafe it is to argue from a few cases to all others. The same character may be a dominant one in certain strains and not in others.[2]

The preceding records and observations are made much clearer by Castle's recent experiments with polydactylous guinea pigs. There was born of normal parents a male guinea pig with an extra toe on the left hind foot. The toe bore a claw, which was not connected to the foot by appropriate muscular and tendinous connections.[3] From the polydactylous male were obtained 15 individuals with extra toes out of a total of 77 offspring. In subsequent generations, partly inbred, the number of extra-toed offspring varied. When the male was paired with females from families in which polydactylism was not known, there were produced about 6.25 per cent extra-toed young. Females, descended from the original father, that gave the first polydactylous male, gave 25 per cent extra-toed offspring. Females, themselves polydactylous, gave 44 per cent polydactylous young.

Many of the young of the first male had extra toes on both hind feet, and in several cases they were better developed than in the original male. The extra toes were supplied with all the muscles characteristic of functional toes. Castle has traced the descent of this race through five generations, and has obtained some important data regarding the inheritance of the anomaly. He finds that the "potency" of certain individuals is a more important factor in the transmission of their characters than is their

[1] *Edinburgh New Philosophical Journal*, 1863.

[2] Several other cases of inherited polydactylism are given by Gregg Wilson.

[3] The same father that produced this "sport" subsequently produced also five others out of 147 offspring.

ancestry. If the various sires are arranged "in the order of the respective amounts of polydactylous ancestry which they possess, we see at once that this is not the order of their potencies, for those having the same amount of polydactylous ancestry often differ much in the potency with which they transmit the polydactyl character."

When polydactylous individuals were mated with normal ones, the results were far from being uniform. Some of the offspring have the extra toes greatly weakened; in other cases there is no toe at all, while in still other cases the extra toe may be fairly well developed. "The inheritance is neither sharply alternative (Mendelian) nor completely blending." It is clear that in its inheritance the extra toe of these guinea pigs does not follow Mendel's law. Castle concludes that the extra toe is inherited in a manner intermediate between blending and alternative inheritance. The gametes, he thinks, only partially blend in the zygote, producing a variable result. "If the inheritance were sharply alternative, we should expect to get, not a series of graduated forms, but two or at most three sharply distinct groups, but this is not the result observed. If, on the other hand, the inheritance were fully blending, all the offspring of two pure parents, or of two cross-bred parents should be alike, but this is not the result observed. We are forced to conclude, therefore, that there occurs a partial blending of gametes [characters] in the zygote, and a partial segregation as the zygote gives off gametes."

Castle points out, further, that partial blending is the more common result of hybridizing, since both sharply alternative inheritance and complete blending are rare. By selection the breeder is able to produce an almost pure race by picking out the more potent individuals in each generation. It is interesting to note that the potency of the male is a germinal variation, tending toward determinate inheritance, and not simply an extreme fluctuating variation due to external conditions. Hence, in selecting prepotent individuals the process involves the choice of certain individuals that transmit certain qualities in a high degree,

rather than involving the selection of extreme somatic fluctuations. These two kinds of selection may be superficially similar, but involve in reality an important difference in principle.

Experiments with Poultry

The different breeds of poultry have furnished Bateson and his co-workers with excellent material for experimental study. The domesticated breeds differ not only in color, but also in the character of the combs, in the feathered or unfeathered condition of the shanks, in the number of toes, in crested and uncrested heads, and the habit to sit or not to sit on the eggs. These characters are inherited discontinuously, showing dominance and recessiveness, and also often giving the Mendelian ratio.

In his earlier work (begun in 1898 and published in 1902), Bateson used principally Indian Game and white Leghorn, but subsequently brown, and white Dorkings and one Wyandotte were used. He found that as a rule pea comb, rose comb, and extra toe are dominant characters, while single comb and normal foot are recessive. Nevertheless, the first generation sometimes shows blending in various degrees, and in consequence the dominance may be considerably reduced. When the F_1's are inbred, some of their offspring show one character, and others the other "in proportions following Mendel's law with some consistency," but here again the results do not always conform to the expectation. Other conflicting results are also recorded that are difficult to explain.

In a recent communication (published in 1905) by Bateson and Punnett further details are given; and in a supplementary paper by C. C. Hurst, some experiments with Leghorns, Houdans, black Hamburgs, and buff Cochins are described. As the results of Hurst are more easily presented in a less technical form, I have relied on them mainly in the following account.

The leaf comb of the Houdan is dominant over the single comb of the Leghorn and Cochin. In a few cases the dominance is complete, but in the majority of cases it is incomplete — intermediate combs being produced.

FIG. 9. Showing single comb, Fig. 1; Pea comb, Fig. 2; Rose comb, Fig. 3.

The Hamburg rose comb is dominant over the single comb of the Leghorn and Cochin, the dominance being complete.

The Hamburg rose comb is dominant over the Houdan leaf comb, although the latter, as stated above, is itself dominant in other combinations. In the second generation (F_2) the Mendelian expectation is largely realized.

The white plumage of the Leghorn dominates over the black of the Houdan and Hamburg, and also over the buff of the Cochin. In only a few cases, however, is this dominance of white complete. In the majority of cases it is incomplete, the white feathers being ticked with black, or there are patches of buff or brown. A few exceptional cases were noted where white did not appear to dominate.

FIG. 10, A. Buff Cochins. (*Reliable Poultry Journal.*)

The black plumage of the Houdan and the Hamburg dominates over the buff of the Cochin, but incompletely, the black being marked and shaded with brown.

When the hybrid dominant whites (F_1) were mated, the offspring (F_2) were dominant whites and recessive blacks in the proportion of 3.1 : 1. When the hybrid dominant whites (F_1) were mated with pure recessive blacks, there were produced dominant whites and recessive blacks in the proportion of 1 : 1. When the hybrid dominant whites (F_1) were mated with a pure buff, they gave whites and blacks in the proportion of 1 : 1.

The experiments in which animals with the normal number of toes are crossed with races having an extra toe give results of unusual interest. In general, the extra toe (of the Houdan) is dominant over the normal foot (Leghorn, Hamburg, Cochin). In some cases the dominance is complete, *i.e.* the extra toe is full size; in other cases all gradations in the size of the extra toe were found "down to the mere duplication of the nail." The extra toe was found in some cases only on one foot, the other appearing as in the normal. There were some cases in which the normal foot *appeared* to dominate, but whether such cases are real dominance of the normal, or the failure of the extra toe to appear in an individual that has it potentially present can only be determined by subsequent breeding.

When the dominant extra-toed hybrids (F_1) were bred together, they gave dominant extra toes and recessive (apparently normal) individuals in the proportion of 3.8 : 1 ; when the F_1's were bred to pure recessives without extra toes, they gave dominant extra toes and recessives, apparently without extra toes, in the proportion of 1 : 1.5.

There were two exceptional cases of F_1, in which the normal foot seemed to dominate. These were a male and a female. When mated they gave 22 chicks, of which 14 had an extra toe and 8 had normal feet. The result shows that the parent birds are really RD's, since chicks with extra toes appeared when the birds were bred together. This conclusion was confirmed by breeding the cockerel to another pure individual with (reces-

sive) normal feet, which gave 11 individuals with and 13 without extra toes. A similar experiment with the hen (F_1) gave analogous results. Evidently in this case a character usually dominant has become recessive. It is clear that unless great precautions are taken, such cases might easily be put down, in other experiments, amongst the recessives.

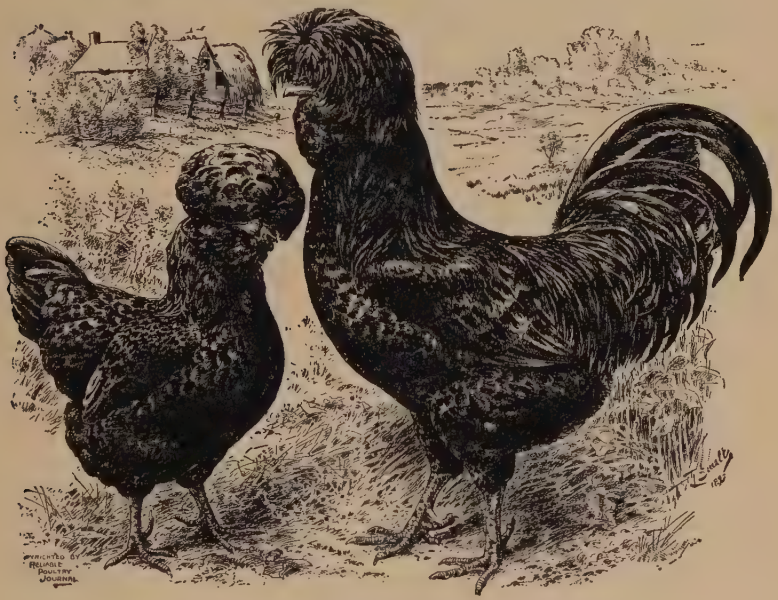


FIG. 10, B. Houdans. (*Reliable Poultry Journal.*)

The shank feathering of the Cochin dominates over the clear shank of the Leghorn, Houdan, and Hamburg, but the dominance is always incomplete. When the F_1's were bred together, they produced a large number of F_2 with feathered shanks, and a few recessive clear shanks in the proportion of 28.7 : 1. The Mendelian expectation is 3 : 1. In other combinations the expectation is much more nearly realized. Hurst concludes that "the Mendelian principles are at work in these aberrant phenomena, but are masked by something not yet perceived."

Hurst's general conclusions are as follows: Dominant characters are rose comb, white plumage, extra toes, feathered shanks,

white and blue shanks, crested head, brown egg color, and broodiness; while leaf comb, single comb, black plumage, buff plumage, normal foot, clear shanks, uncrested head, white egg color, and non-broodiness are all recessive to the dominants given above. *Some of these recessives may, however, be dominant over others.* Thus leaf comb and black plumage are dominant over single comb and buff plumage that remain recessive.

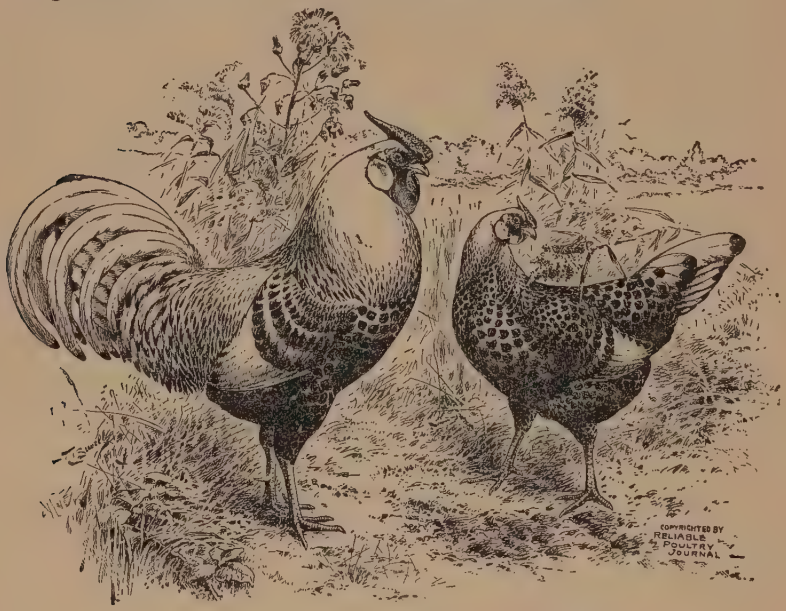


FIG. 10, C. Silver-spangled Hamburgs. (*Reliable Poultry Journal.*)

Hurst points out further that dominance may be *complete*, when it is indistinguishable from pure dominance, or incomplete, showing the influence of the recessive character in different degrees. For some characters the dominance is always complete; in some it is always incomplete; and in others it is sometimes complete, but more often incomplete. The incomplete dominants appear to be about twice as numerous as the complete.

In the second generation F_2 the dominants are again complete and incomplete.

It is to be remembered that all the preceding characters behave

independently of each other, there being no correlation between the characters usually associated with a particular breed, so far as their inheritance is concerned.

One of the most curious results in crossing black and white fowls is the occasional appearance of a blue (or Andalusian) color, which consists of a minute patchwork of black and white. It has been known for some time that this color does not breed true, but a pair of such blue fowls gives rise to 25 per cent black, 50 per cent blue, and 25 per cent white. The explanation of this is that the germ-cells of the blue individuals are black and white, hence the result; but the special condition that leads to the occasional formation of blue by the combination of black and white is not known. Possibly the presence of latent colors determines the result.

The most recent experiments with poultry are those of Davenport. His work confirms many of the results already obtained by Bateson and Hurst, and also establishes the relation of dominance and recessiveness for some new characters. It is these latter points that will be especially considered here.

A cross was made between the single comb, black Minorca and white-crested, black Polish. These races and their hybrids are shown in Fig. 11; 1–6. In the hybrid (5 and 6) the comb is single anteriorly and bifurcated behind. There is much variety in the extent to which the comb is split. In fact, it was single in one case. Neither parent type can be said to dominate, the Minorca having a large single comb, and the Polish a much-reduced bifid comb. Davenport suggests that these two types of comb may both be dominant types that combine to form the Y-shaped comb. When the hybrids were inbred, there resulted, in a total of 101 offspring, 29.7 per cent showing single comb, 46.5 per cent Y-shaped comb, and 23.8 no comb (or only papillæ). Two interpretations are possible. On the assumption of two dominant and two recessive types, viz. (1 a) median comb and (1 b) no median, and (2 a) no splitting and (2 b) splitting, the results agree more or less with the expectation. But on another assumption the results conform even more closely, viz. if we

assume that single comb and V-shaped comb (that of the Polish) are contrasted characters, and the Y-shaped comb is a combined

FIG. 11. Male and female black Polish fowls, Figs. 1 and 2; male and female black Minorca, Figs. 5 and 6; and hybrids, male and female, Figs. 3 and 4. (After Davenport.)

form constantly reproducing itself. Further work must decide between these alternative views.

This idea of combined dominance was first suggested by Bateson and Punnett to explain the walnut comb of certain hybrids. Thus when rose comb and pea comb are crossed, walnut comb results. The gametes produced by these hybrids are of four types and in equal numbers; namely, single, rose, pea, and walnut, giving when inbred 9 walnut (rose-pea), 3 rose, 3 pea, 1 single comb. The interpretation offered by Bateson and Punnett for these facts is that the characters of the original parents with rose and pea combs are rose and no pea, and pea and no rose. The contrasted characters are rose and absence of rose, pea and absence of pea. When rose and pea bearing gametes meet, the walnut comb is produced. The results follow the rule for two characters. In other words, rose and pea combs are not themselves contrasted characters, but the allelomorph of each is its absence. The authors point out, however, the danger involved of making general assumptions of this sort when two characters meet.

The nostrils of the Minorca are slitlike, and this dominates the wide-open nostril of the Polish, but the dominance is imperfect in the first hybrids. In the next generation, F_2, the split nostril is present in 21 per cent, but even in this generation the high or dominant nostril is frequently imperfect.

The Polish fowls have a large cerebral hernia on the top of the head, covered by a hardened layer of outer brain coat or dura mater, and by the skin. The Minorca breed has a normal head. In the hybrids, F_1, not a single case of hernia occurred, but most of them showed evidence of their mixed ancestry in the presence of a frontal eminence. In the second hybrid generation, F_2, the hernia reappears again in 23.5 per cent of cases — a close agreement with Mendelian expectation.

A crest is present in all the hybrids, but always reduced in size. "The crest is dominant, but dominance is imperfect." The crest is larger in the female hybrids, as it is in the female Polish breed. In the second hybrid generation the crest was absent in about 30.7 per cent.

Davenport concludes that in this cross the dominance is incom-

plete in all cases; the nearest approach to typical Mendelian inheritance is exhibited in the crest, but in the first generation it is always reduced. The white color of the crest is recessive in the male hybrids, but is not entirely absent in the females. The high nostril is recessive, yet it shows its influence in the first hybrids. The comb in the first hybrids is different from that of either parent, yet in the second generation there is a partial return to the two parent types.

An interesting cross was made between the Japanese long-tailed fowl or Tosa fowl (Fig. 12; 2) and the white Cochin Bantam (Fig. 12; 1). In the Tosa fowl the feathers of the tail show continuous growth, reaching in extreme cases 18 feet, and generally 7 to 8 feet.

There is a marked sexual difference in the Tosa breed, but not in the white Cochin. The male hybrids had the coloration of the Tosa cock except that every feather was barred with white (Fig. 12; 3). The female hybrids were like the Tosa hen, excepting that the shafting was much broadened, and the saddle feathers and the secondaries were black and buff barred. In the second generation the two original types reappeared. There were 28.1 per cent white (Fig. 12 : 4) and 71.9 per cent pigmented individuals. However, of the whites, only five were without reddish pigment, showing that they were contaminated by the cross. "The 41 pigmented individuals showed a curiously mixed lot of coloration. Of 41 mature *females* 6 are like the female Tosa fowl, without barring, but sometimes with wider shafting than the male Tosa fowl. The remainder have feathers of the back and wing coverts barred with lighter, even with white — a condition not found in the female first hybrids. One of these shows a mixture of female Tosa and female Partridge Cochin coloration. As no Partridge Cochin is involved in the immediate ancestry, this looks like a 'reversion'; the characteristic has probably lain latent in the White Cochin. Of 10 *males*, 2 showed no trace of white, and may consequently be considered as homozygous. The remainder are more or less barred with white. One bird shows a remarkable mixture of Tosa and male Partridge Cochin coloration." The

statement shows besides the contamination of the second generation the complexity of the result due to latent characters other than those patent in the breeds used.

In regard to tail length, it was found that the first hybrid

FIG. 12. White Cochin Bantam, Fig. 1; male Tosa fowl, Fig. 2; hybrid, F_1, male, between last, Fig. 3; second generation hybrid extracted recessive, Fig. 4. (After Davenport.)

males developed abnormally long middle-tail feathers, but the tail was not so long as in the Tosa fowl.

It will be observed that in this cross white is apparently not dominant, as it is as a rule in other combinations; but evidence of the white is seen in the barred feathers of the first hybrids.

"The white Cochin has no sexual dimorphism in plumage color, while the Tosa fowl is strongly dimorphic. Every one of the first hybrids is dimorphic in plumage coloration, the two sexes resembling, except for the white, respectively the female and the male Tosa fowl. It is striking to see how from a germ-cell of the male Tosa fowl either a bird colored like the male Tosa or a bird colored like the female Tosa may arise. The male germ-cells contain the Anlagen not only of the male characteristic but also of the female characteristic."

In another case two races, *both* having sexual differences, were crossed. These were the Tosa and the dark Brahmas. The hybrids were also sexually different, showing the dominant color of their respective sex. Thus the red wing-bar and white wing-bar are found in the males, and the shafting and penciling of females in the female hybrids.

There are two races of fowls that have aberrant feathers. In the *Frizzled fowl* (Fig. 13; 2) the contour feathers have a shaft convex inward so that the feather is lifted up and even turned forward. The primaries of the wings show groups of the barbs that are twisted in corkscrew fashion. In the *Silky fowl* (Fig. 13; 1) the contour feathers are like down feathers, with a weak shaft, and the barbs are subdivided, producing a fluffy effect. The quill feathers of the wing and tail are less modified. The Silky fowls used in the experiments were white, the Frizzle were dark (black, red, and buff).

Some of the hybrids were white (Fig. 13; 4) and some were dark (77.4 per cent). Here the white is neither dominant nor recessive, but the explanation of the result is not clear unless one or both races are impure in their color inheritance. None of the hybrids showed any silkiness, which is, therefore, seen to be recessive to non-silkiness. Only 6 of the 10 hybrids were frizzled, the other four having flat feathers. Davenport explains this approach to equal numbers on the ground that his frizzled animals produced both frizzled and plain bearing germ-cells.

In another cross the breed of black-breasted red Game (Fig. 14; 2), in which the tail and rump are entirely absent, was

crossed with the white Leghorn breed (Fig. 14; 1). Of 24 hybrids, 12 were white (Fig. 14; 3), or prevailingly so; black was usually present, and more rarely some buff. The other 12 hybrids were

FIG. 13. Silky fowl, Fig. 1; Frizzle fowl, 2; extra toe, Fig. 3; hybrid, F_1, between Silky and Frizzle, Fig. 4. (After Davenport.)

black and white barred, or black with reddish. The tail and rump were normal. Rumplessness is recessive in the strain used by Davenport.

Aside from the details of Davenport's work, his chief results consist in showing that in nearly all characters examined the influence of the recessive character is to be seen in the first hybrids, and even in the second hybrids, so far as obtained, the

FIG. 14. Single-comb White Leghorn, male, Fig 1; rumpless Game male, Fig. 2; hybrid, F_1, between last two races, Fig. 3.

impurity of the offspring is often apparent. As yet in only a few cases have the experiments been carried to the second generation. The results are evidently complicated by the impurity of some of the strains that were used and by the presence

of latent characters in these strains. Despite the fact that some of the birds were bought as "pure" stock, *i.e.* stock that breeds true as long as inbred, yet the presence of latent qualities in them is admitted. Under these circumstances it does not seem to me "contrary to experience" to admit that "pure" strains carry latent characters.

Davenport contrasts the dominance *versus* the recessiveness of new characters with the original characters of fowls as indicated by their presence in the wild parent species of Indian game and of Aseel. He finds that the new characters dominate as often as they are recessive. Hence there is no reason to suppose that new characters are at a disadvantage in respect to dominance as contrasted with old characters.

Experiments with Pigeons

Darwin has given the results of several experiments in crossing pigeons. There are also several other recorded results of hybridizing races of pigeons. The hybrids (F_1) appear to be variable in color, but some of the markings peculiar to the wild Rock Pigeon are apt to appear. For example: A male "Nun" that is white, with head, tail, and primary wing feathers black, was crossed with a red "Tumbler." Neither parent had any blue in the plumage, nor bars on the tail or wings. Of the several young, one was red over the back, but the tail was as blue as that of the Rock Pigeon; two others were quite similar; a fourth was brownish and the wings showed a trace of a double bar; a fifth was pale blue over the back, breast, and tail, but the neck and primary wing feathers were reddish; the wing had two distinct red bars.

When a black "Barb" was crossed with a red "Spot," the young were black, or dark, or pale brown, sometimes slightly piebald with white. Six of these birds had double wing bars, etc. When a black Barb was crossed with a snow-white Fantail, some of the hybrids were black with a few white feathers, others were dark, reddish brown, and others snow-white. None of them had wing bars.

These and other experiments with pigeons show that the results are more complicated than in the case of fowls. It is not possible to bring the results under a single point of view at present. Ewart's experiments[1] with pigeons indicate that while certain kinds of crosses may give rise to offspring resembling the Rock Pigeon, yet in other cases a more immediate ancestral color may come out. A dark blue Fantail, having all the characteristic bars of the Rock Pigeon, was bred to a less pure blue Fantail. On two occasions an absolutely pure white Fantail was produced. This result, Ewart thinks, is due to a reversion to a white grandparent. Ewart also crossed a white Fantail with a white Pouter. The offspring was white in color, but in form resembled the Pouter. A hybrid between an "archangel" and an "owl" was bred to a white Fantail. The two offspring were blue, one of them being almost identical with the wild Rock Pigeon, more especially with the Indian variety. Not only was there reversion in color, but in form as well.

Ewart seems to think that reversion amongst closely inbred races of dogs, horses, and pigeons leads to a sort of rejuvenescence of the stock. Those individuals showing the ancestral characters prove to be stronger and more active.

The reversion to the type of the Rock Pigeon, that seems to play often so conspicuous a rôle in these experiments with pigeons, recalls the return to the gray color in mice when fancy breeds are crossed, but in the second generation of mice there is a return in some of the forms to the parent types. How far this occurs in pigeons is not clear from the evidence at hand.

A brief but important note in alternate inheritance in pigeons is given by Staples-Browne. Webfoot sometimes suddenly appears in pigeons. A pigeon of this sort crossed with another having normal feet produced six normal-footed offspring. These individuals (F_1), inbred, produced in one case nine with normal feet and three with webbed feet. Another pair (F_1), however, produced seventeen normal birds. Extracted web-footed individuals produced six web-footed. It appears that the latter condition is recessive to normal feet.

[1] The Penycuik Experiments.

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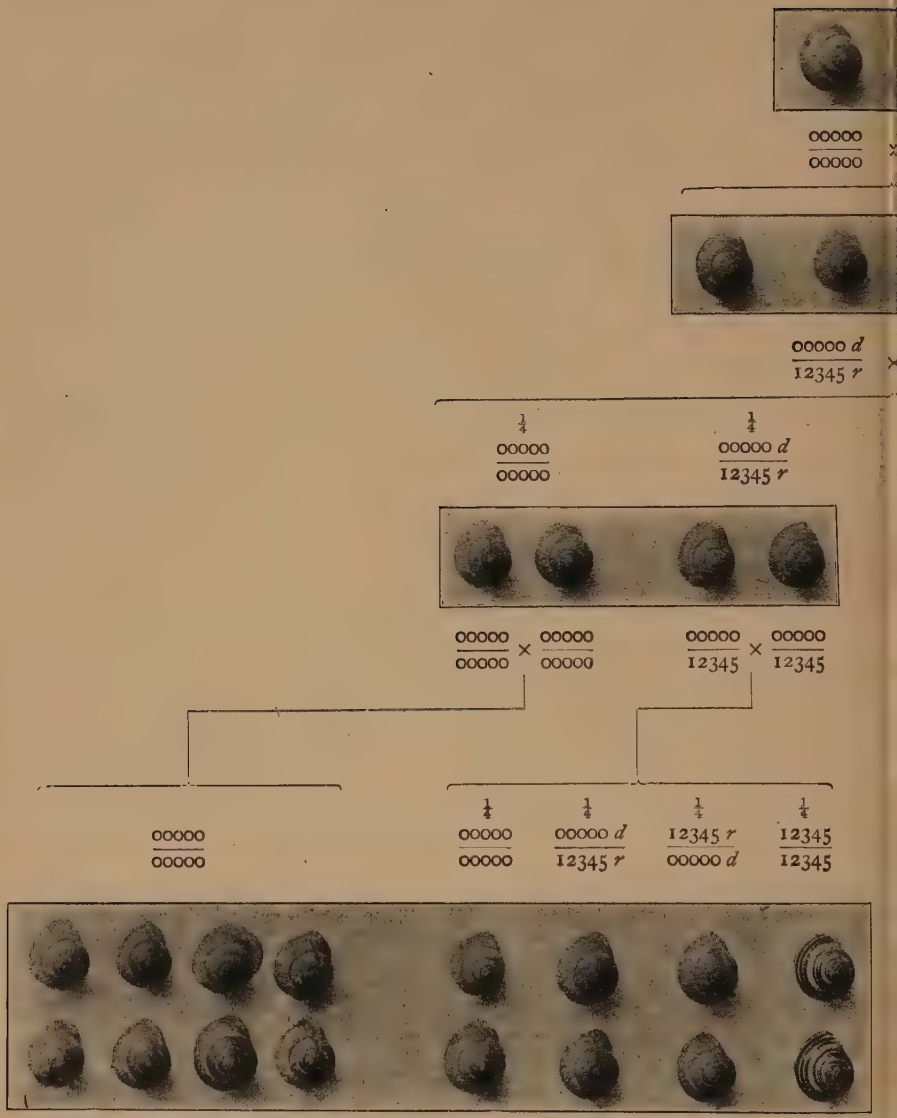

FIG. 15. Helix hortenses. First (top) line, a bandless and a banded shell. When indivi these are inbred they give bandless and banded (third line) in the proportion of 6 to 2 (*i.e.* 3 sives, as shown by inbreeding (fourth line). (After Lang.)

$\frac{5}{5}$

$0\,d$
$5\,r$

$\frac{1}{4}$ $\frac{12345\,r}{00000\,d}$ $\frac{1}{4}$ $\frac{12345}{12345}$

$\frac{12345}{00000} \times \frac{12345}{00000}$ $\frac{12345}{12345} \times \frac{12345}{12345}$

$\frac{1}{4}$ $\frac{1}{4}$ $\frac{1}{4}$ $\frac{1}{4}$

0000 $\frac{00000\,d}{12345\,r}$ $\frac{12345\,r}{00000\,d}$ $\frac{12345}{12345}$ $\frac{12345}{12345}$

0000

these two kinds are paired the first generation (second line) are all bandless. When
f these two are extracted dominants, four are dominant-recessives, and two extracted reces-

CHAPTER IX

EXPERIMENTS WITH SNAILS, MOTHS, AND BEETLES

The European snails, *Helix hortensis* and *Helix nemoralis*, have been studied by Lang, whose experiments in breeding them have extended over several years and, though still in progress, have already yielded decisive results on a number of important points. The young snails require at least two years, generally three, and often four years to reach maturity. The animals, although hermaphroditic, do not self-fertilize, as isolation experiments have shown. The sperm, received during copulation, may remain alive for several years in the receptaculum seminis, therefore wild individuals cannot be used safely in breeding experiments, but the young snails must be first reared and isolated and paired in order that the parentage of their offspring can be certainly known.

The bands of pigment on the shell are the chief characters that Lang has studied in his experiments. Colonies of snails are sometimes found in which only two kinds of individuals are met with, — those with five bands and those without bands, no intermediate types existing in such colonies. These colonies furnish the best materials for breeding experiments. In such colonies the banded individuals are "pure," that is, they breed *true* to their type. It is more difficult to obtain "true" individuals without bands. Those are most likely to breed true that are found in colonies in which only bandless individuals exist.

If virgin banded and bandless individuals are allowed to pair and are then separated, each will make a nest in the ground and deposit from 40 to 60 eggs, or more. The banded indi-

viduals may be designated by $\frac{12345}{12345}$, and the bandless by $\frac{00000}{00000}$. The young of the first generation are all without bands. In other words, the banded condition is the recessive. The formula used by Lang for these individuals is $\frac{00000\,d}{12345\,r}$.

When the individuals of the first generation (F_1) are paired, the offspring of the second generation are of two sorts (like the grandparents). Those having the dominating character (bandless) are to those with bands as 3 to 1. In other words, the Mendelian ratio appears. That this is really the case is shown by further experiments. The banded individuals are the recessives, $\frac{12345}{12345}$, and produce only banded offspring. The bandless are of two kinds, one third true or "pure" dominants, $\frac{00000}{00000}$, and two thirds dominant recessives, $\frac{00000}{12345}$. There are no external characters that distinguish the pure dominants from the dominant recessives, since both are bandless; but if they are separated in pairs and their offspring obtained, it will be found that in some cases all of the offspring will be bandless. They have arisen by the union of two extracted dominants, $\frac{00000}{00000} \times \frac{00000}{00000}$, or by the union of one extracted dominant and of one dominant recessive, $\frac{00000}{00000} \times \frac{00000}{12345}$. In other cases two thirds of the offspring are bandless and one third banded, showing that two dominant recessives have paired, $\frac{00000}{12345} \times \frac{00000}{12345}$.

Lang has also carried out some experiments with snails in which two characters are involved. The individuals of Helix nemoralis or of H. hortensis differ not only in their banding but also in the color of the shell, which may be yellow or red. These colors also form a pair of antagonists that follow the Mendelian law. The double combination of banded and bandless, yellow and red, gives the Mendelian expectation for two contrasted characters.

Individuals of these two species also show other antagonistic characters. There are size differences, and these also Mendelize. The form of the navel also differs and gives a fourth character.

The preceding breeding experiments relate to differences within the species, but Lang has also carried out experiments between the two species, H. hortensis and H. nemoralis. The results will be described in the next chapter. One point of interest must, however, be mentioned here. As stated above, each species contains individuals that are banded or bandless, red or yellow, etc. These are varietal differences. The point of interest is that when the two species are crossed the offspring — species hybrids — show that one of the antagonistic characters dominates in the same way as when the varieties within the species are crossed. For example, if a bandless individual of Helix hortensis is paired with a five-banded individual of Helix nemoralis, the hybrids are in some cases entirely bandless, in other cases partly bandless and partly five-banded. Lang accounts for these results by assuming in the first case that a "pure" bandless form was used, all of whose germ-cells were "pure" and hence dominated; while in the other case a dominant recessive was used which would produce both kinds of germ-cells. On the other hand, one should not lose sight of the fact that the hybrid-crossing may itself set "free" latent characters, as in mice, so that the results may have arisen in this way. Lang concludes that those varietal characters that Mendelize within the species behave in the same way when different species are crossed.

Experiments with Silkworms

Elaborate series of experiments with silkworms have been carried out by Coutagne.[1] The results of ten years' work were published in 1903. Although ample evidence is furnished of *alternative* inheritance, the results are not treated by the author from the point of view of Mendel's law, although there are indications in many places that some at least of the results might profit-

[1] *Bulletin Scientifique de la France et de la Belgique*, XXXVII, 1903.

ably have been thus considered. On the other hand, there are also numerous instances where it seems probable that the inheritance is of a different kind. To what the results are due is not clear in all cases, but it seems not improbable that some of the domesticated races of silkworms have originated from different wild species, or even genera; while others have arisen under domestication as sudden variations. Several instances of this sort are given and invite special attention. Some of the races may be crosses, *i.e.* hybrids, and even although breeding true *inter se* the individuals may carry in a latent state the qualities of other strains. In the light of these possible complications we can do little more than examine Coutagne's results as they stand. It is to be hoped that this most promising field of inquiry may be further investigated.

Coutagne distinguishes between (1) an "alliage homogène," or *fusion*, in which the hybrid character is something new and intermediate between the parental characters (which are united or fused "fondus"); (2) a "mélange hétérogène," or *mixture*, in which some of the hybrids are like one parent and some like the other in respect to a particular character, and still others intermediate; (3) a "liquation" or *separation* in which there is no fusion of characters in any of the individuals, but they are strictly like one or the other parent type.

The inheritance of the following characters was examined by Coutagne: —

1°	The caterpillars ("worms"):	
	White (with or without a masque)	a, 1 mode *albus*
	Black	a, 2 " *niger*
	Zebra	a, 3 " *virgatus*
2°	The cocoons:	
	Yellow	b, 1 " *flavus*
	White	b, 2 " *niveus*
3°	The moths:	
	White, with or without "cendre" markings	c, 1 " *canus*
	Black	c, 2 " *casteneus*

Coutagne states that any one of the three kinds of larvæ, white, black, or zebra, may be associated with either of the two kinds of cocoons, yellow or white. This gives six combinations. Any of these six may be associated with either of the two kinds of moths, white or black, giving a total of twelve possible combinations. The following results were obtained: —

(1) Crossing individuals with two different characters often gives offspring in the first generation that are intermediate in character. Thus the race Chang-hai has a white cocoon that is small and spherical, while the race Jaune Var has a rose-yellow cocoon that is large and ellipsoidal with a constriction. The cocoons of the hybrid have a pale yellow tint, about intermediate in color,[1] the form also is intermediate — ellipsoidal, but less elongated, and the constriction absent or scarcely marked.

(2) Crossing individuals of different races may give in the first generation a *fusion* of two characters, but subsequent generations descended from the first show a *mixture* of the two characters in question.

The statement is also illustrated by reference to cocoon-characters, but the line of separation of the colors does not appear very sharp.

(3) When the crossing has given a *fusion* in the first generation, and in the second generation a *mixture* ("mélange hétérogène"), it is possible to produce a homogenous race, by means of selection, that shows the characters that fused. In each successive generation the individuals presenting the united characters, *i.e.* those "fondus," must be selected. This statement Coutagne puts in the form of a question, because he has not, he says, indisputable facts in support of it.

(4) Crossing individuals with different characters often gives a separation in equal parts of the two characters. For example, an individual of a race having white worms, white cocoons, and white moths was crossed with an individual of a race having

[1] Two to three per cent, however, were pure white, small, and spherical (type Chang-hai); and 4 to 5 per cent were yellow, nearly of the yellow type but less yellow. These Coutagne suggests were due to accidental mixing.

striped worms, yellow cocoons, and black moths. The results are shown in the table, in which the horizontal lines represent the stages of each individual.

No. of Individuals	Worms	Cocoons	Moths
116	striped	yellow	black
124	white	yellow	black
111	white	white	black
108	striped	white	black

Thus there are nearly equal numbers of white and striped worms (235 and 224); the same holds nearly for the two characters of the cocoons (240 and 219). No worms intermediate in color were found nor were there intermediate conditions between the cocoons.[1] It will be seen that all the moths were black (melanitic), yet Coutagne thinks some influence of the white was present.

(5) Crossing individuals with different characters gives at times offspring all like one parent, without the other character showing any influence in the first generation. For example, an individual of a race with *white* worms, cocoons, and moths was crossed with an individual having white worms, but *yellow* cocoons and black moths. All of the cocoons were white.

An individual of a race having black worms, white cocoons, and moths was crossed with an individual having white worms, yellow cocoons, and black moths. All of the cocoons were white.

An individual of a race having *black* worms, white cocoons, and white moths was crossed with an individual having white worms, yellow cocoons, and black moths. All the worms were black, about half the cocoons were yellow and half white (262 and 248), without any intermediates. All the moths were black or blackish, but rarely one was almost white.

In a third case an individual of a race having black worms, white cocoons, and white moths was crossed with an individual

[1] Certain double cocoons that were rejected did not show intermediate colors.

having white worms, yellow cocoons, and white moths. All of the worms were black, half of the cocoons were yellow, and half were white (180 and 188), without any intermediate ones.

In a fourth case an individual (female) with white worms, cocoons, and moths was crossed with another (male) having black worms and moths, but yellow cocoons. All the cocoons were white. The worms were 265 black like the father and 253 white like the mother; some of the moths were white, others black, others intermediate. In the group of 265 black worms there were no more black moths than in the group of 253 white worms. Thus the characters black or white worms and the characters black or white moths have no mutual relation.

In a fifth case, the female of a variety "Jaune Var" was used that has the black character of the worm and of the moth almost completely "fixed," but fixed only recently, while the yellow of the cocoon had been fixed for a long succession of generations. The male was of the race "Blanc des Alpes" and had white characters throughout. The result of the cross gave white cocoons, the *paternal type* — the reverse of what occurred in other cases where the white was maternal. The worms were 258 white like the father and 182 striped like the mother (3 to 1). This predominance Coutagne attributes "to the ancestors of the white worms of the mother; possibly if the striped character had been fixed for a greater number of generations there would have been an equality between the white and striped worms." The questionable character of this explanation is at once apparent in the next experiment that Coutange gives, in which the same types were crossed as before and all the worms were striped.

(6) It has been found that white cocoons dominate over yellow, but in another combination the reverse was found to be the case, showing that there is no absolute rule for all races in regard to the inheritance of white *versus* yellow.

(7) After crossing individuals of two races which give offspring showing the character of one parent, it often happens that the concealed character reappears in the following generations.

When Blanc des Alpes are crossed with Jaune Var, all the offspring have yellow cocoons. The next generation gave yellow and white cocoons with none intermediate; the proportion of yellow averaged in fifteen lots 75.2. Here there seems to be an approach to one fourth that strongly suggests the Mendelian ratio. In other cases, however, an average of 49.3 per cent was obtained. The evidence here is opposed to this interpretation, unless one of the races itself had a latent character that did not appear until the second generation.

(8) When two crossed races give a separation in equal parts of the two characters, the following generations give equally again the separation of the two characters without its being possible to realize their *fusion* in a single individual.

For example, two types were crossed, each having striped worms and yellow cocoons. The offspring gave four classes: —

		Worms	Cocoons
1	236	striped	yellow
2	80	striped	white
3	89	white	yellow
4	34	white	white

In another case the female belonged to a race with white worms and cocoons, the male striped and yellow cocoons. The crosses were: —

		Worms	Cocoons
1	95	striped	yellow
2	84	striped	white
3	103	white	yellow
4	109	white	white

Seven other combinations are given, but until some principle running through these cases can be formulated it is needless to recount all the results here. It is true that Coutagne attempts to show that the rule in subsequent generations is such that the inheritance of the contrasting characters follow the sequence of

$\frac{1}{2}, + \frac{1}{4}, + \frac{1}{8}, + \frac{1}{16}$, which is the same as Galton's law, but so far as I can interpret his data this is not strikingly apparent. Failing to carry the results discussed above through subsequent generations leaves the matter in an unsatisfactory condition. In only one experiment is the result of the next generation given, which shows, if I interpret it correctly, that each of the four types gives, when inbred (?), individuals amongst which most of the same types reappear, but in very different proportions; the most striking result being that each type gives a much higher percentage of its own kind.

(9) In the course of separation of two characters which takes place during a series of generations it happens at times that when two similar individuals are paired, *i.e.* both having the same character, the other contrasted character never appears again in their descendants. It has not simply become latent, but has gone entirely.

It is obvious that this would happen, according to Mendel's formula, whenever the individuals are pure dominants or pure recessives.

(10) Crossing individuals with different characters often gives in the first generation a mixture, "mélange hétérogène," of two characters with marked predominance of one of them in the combination, and in this case it is easy, by means of selection in successive generations of the individuals having the most marked character, to fix rapidly this character and even to exaggerate its relation to the other.

In cases of this sort it is not clear that Mendel's law holds at all, and some other principle must be involved, especially if the author means that the results are obtained by simply discarding the individuals having the disappearing character and allowing the rest to breed together.

(11) Crossing two individuals with a different character often gives in the first generation a separation of these characters in a part of the offspring and in the other part a union constituting a new character. Subsequent generations show a separation or *liquidation* of these characters.

For example, a female of a race with black worms and white cocoons was mated to a male with striped worms and yellow cocoons. The offspring were: —

No. of Individuals	Worms	Cocoons
89	black and striped	yellow
86	black and striped	white
77	black	yellow
77	black	white

The mother had been a white moth, the father a black moth. The offspring (of this table) consisted of a small number of whites, and the majority of a "gris-marron ou moues foncé," in other words, a mélange hétérogène of the white and the black character, but without predominance of either.

"The fact of greatest interest in this cross is the fusion, or at least the close juxtaposition, of the black and the striped characters in half of the caterpillars of this lot. These worms at the same time black and striped are most curious and constitute a new character without any intermediate."

The further evolution of these new types was as follows: The group with black-and-striped worms and yellow cocoons gave:—

No. of Individuals	Worms	Cocoons
127 { 90 individuals	black and striped	yellow
127 { 37	black and striped	white
47 { 29	black	yellow
47 { 18	black	white
20 { 13	white	yellow
20 { 7	white	white
129 { 66	striped	yellow
129 { 63	striped	white

The group with black-and-striped worms and white moths gave:—

No. of Individuals	Worms	Cocoons
259 { 70	black and striped	yellow
259 { 189	black and striped	white
88 { 27	black	yellow
88 { 61	black	white
34 { 11	white	yellow
34 { 23	white	white
116 { 39	striped	yellow
116 { 77	striped	white

Coutagne calls attention to the reappearance of the white character that is atavistic on his interpretation. It will be noticed in each group the numbers are nearly exactly halves, thus 70 and 189, 27 and 61, 11 and 23, 39 and 77.

Although it is not apparent that an application of the Mendelian law is competent to explain all the results of these experiments, it is probable that some such rule lies behind several of the observed cases. Other cases clearly show blended inheritance, and still others show in some characters one kind and in others other kinds of inheritance. It is difficult in many cases to understand just what really occurs, but the results show plainly how complicated the problem of inheritance in a single group of forms may be.

In a note published later, Coutagne compares his results with the Mendelian formula and points out that certain classes of his results conform to this law. It seems to me not improbable that if the latent qualities of some of the races be taken into consideration, the conformity may be greater than Coutagne admits. On the other hand, it appears probable that some characters do not dissociate according to the Mendelian expectation.

A short paper by Toyama on Mendel's law as applied to silkworm crosses has very recently appeared, in which it is shown that many of the same characters studied by Coutagne give the Mendelian expectation. Unfortunately no reference is made to Coutagne, although a comparison would have been valuable.

When moths of the Siamese breed, having either yellow or

white cocoons, are crossed, the offspring (F_1) produce only yellow cocoons. When these hybrids are inbred they give two kind of individuals; namely, those producing white and those producing yellow cocoons in the proportion of 25.03 per cent whites to 74.96 per cent yellows. The whites are extracted recessives, and are found to breed true. The yellows are of two kinds, one kind giving only yellow-producing offspring (the extracted dominants) and the other kind producing yellow as well as white in the proportion of 3 to 1 (the dominant recessives). A more complex result was obtained when Japanese "whites" and Siamese "yellows" or when Japanese "whites" and European "yellows" are paired. The first generation give offspring that produce yellow cocoons. When these individuals are paired, they give in the second generation four kinds of cocoons: (1) pure yellow, 70 cases; (2) pale pinkish yellow, 21 cases; (3) greenish white, 24 cases; and (4) pure white, 12 cases.

The results show apparently that we have to do here with three characters, one of the races used being a monohybrid and the other a dihybrid. In subsequent generations the pure white type breeds true. Some of the yellows give only yellows; others give white (25 per cent) and yellow (75 per cent); others give yellow (75 per cent), flesh-colored (25 per cent), and still others white and greenish white (25 per cent), yellow (56 per cent), and flesh-colored (19 per cent).

The flesh-colored forms of the second generation gave white (25 per cent) and flesh-colored (75 per cent). The greenish white type of the same generation gave white and greenish white offspring.

Toyama used two breeds of caterpillars, pale whites characterized by the absence of markings, and striped whites having dark stripes. The former breeds true, while the latter produces some pale whites and is therefore a cross breed form. The hybrids produced by uniting these breeds were white and striped worms in equal numbers. In subsequent generations the whites remained true while the striped kind gave both whites and striped.

Other crosses were made between a brood showing no markings and yellow cocoons, and striped with white cocoons, and gave the usual Mendelian results of splitting and recombination.

Experiments with Beetles

In the Californian beetle, Lina lapponica, two types exist, a spotted type shown in Fig. 4 and a black type shown in Fig. 6. The heredity of these two types has been studied by Miss McCracken. When the beetle emerges from its pupal case the wings are nearly pure white. The large median black spot and the two lateral spots on the prothorax are present (Fig. 1). In the course of ten minutes faint indications of spots appear on the wings (Fig. 2), and after fifteen to twenty minutes these become more distinct, as seen in Fig. 3. In the course of forty-five minutes the spotted type has reached its final condition (Fig. 4). The black type passes through a stage like that of Fig. 3 to that of Fig. 5, and finally after forty-five minutes to Fig. 6. In a sense the black type passes through the spotted type, the background becoming as dark as the spots themselves, so that the spots can no longer be seen.

If these two kinds of individuals are collected at random and isolated in pairs, it is found that the spotted pairs sometimes (in half the cases) produce their own kind only, and in other cases produce both spotted and black types. There are no intermediates.

When the blacks are paired they produce in some cases broods that are all black, and in other cases broods in which some of the individuals are black and some are spotted, in the proportion of 1 spotted to 1.7 black.

If a black and a spotted individual are paired, mixed broods are produced with a preponderance of the spotted type.

The results for the second generation are especially interesting. If those broods from black parents are picked out in which all of the individuals are black and these are paired, all of their offspring, without a single exception (in 4985 cases), are black. The third generation is also black. Hence there is a pure race of blacks. The black is evidently the recessive form.

The results of the second generation are different when the spotted forms from the pure spotted brood produced by spotted parents are paired. In this case both spotted (1021) and black

FIG. 16. Development of the two-color patterns of Lina Japonica. (After McCracken.)

(345) are produced in the proportion of 3 : 1. In two cases, however, all the offspring (265 in one case, 182 in the other) were spotted. If these are paired, they produce only spotted forms. Clearly we have to deal here with extracted dominants.

The results may be briefly summed up as follows: the two types of beetle show alternate dominance and recession, the spotted character being dominant, the black being recessive. By isolation both types may be obtained "pure." In nature both are continually crossing and recrossing, so that the chances are that most individuals are impure, but by selection pure breeds can be quickly obtained from them.

Experiments with the Currant Moth

There is a curious case, reported by Raynor and Doncaster for the currant moth (Abraxas grassulariata), in which there is a rare variety, A. lacticolor, that had previously been found only in the female sex. The variety is recessive in the first generation when crossed with the parent form. The offspring, however (F_1), produce males, all of which are the ordinary variety grassulariata, and females, half of which are like the males and the other half are var. lacticolor. When, however, a lacticolor female is paired with a (F_1) male hybrid (L ♀ × G (L) ♂), some of the male offspring are lacticolor (and others female). The explanation of the transference to the male of the female character is not apparent.

Experiments with Tephrosia

A series of hybridizing experiments between the moths Tephrosia bistortata and Tephrosia crepuscularia have been described by Tutt (based on records by Riding and Bacot). These two species are sufficiently similar to have been put together as one by some entomologists because occasionally individuals have been found that could not be referred with certainty to either species, but Tutt describes a number of constant differences between the two forms and regards them as distinct. Both species have a melanitic variation, that of T. bistortata

being exceedingly rare and almost confined to South Wales, but that of T. crepuscularia is widely distributed and known as *aberratio* delamerensis. The first generation of hybrids (F_1) is described as containing individuals that are like the one or the other parent form, although each kind may show traces of the other species. Tutt states that he has avoided the use of the term "intermediate" when describing these hybrids because the term has been made to cover so many different things; but that nevertheless all of the hybrids with few exceptions are intermediate to varying degrees, *i.e.* "almost every specimen appeals, in some part of its facies, to a specialist, as resembling T. bistortata, whilst the same specimen, in other particulars, strikes one as resembling T. crepuscularia." When inbred the hybrids produce a large percentage of individuals differing much from either parent-form. The crossing of the hybrids, obtained from original reciprocal crosses, tends to produce a mixed progeny, some referable to known forms of the crossed species, others quite unlike anything ever obtained in nature. . . . These experiments support Eimer's view that sexual combination can lead to the production of new forms. I doubt, however, very much whether they could be perpetrated without selection," for if crossed with one of the present species they would "in my opinion" revert to the wild form.

Some interesting results were also obtained in regard to the sex of the hybrids. "The greater vigor of the male results largely in the production of female offspring. When the male is of the dominant species, females are developed in fair proportion; when the female is of the dominant species, males are largely in excess."

LITERATURE, CHAPTER IX

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CHAPTER X

OTHER KINDS OF HYBRIDIZING

Blended Inheritance

We have seen in the cases that come under Mendel's law that the contrasted characters do not both develop at the same time, the offspring in the first generation being often like one or the other parent. Yet in some of these cases there is evidence that the dominant character may be weakened by the recessive one. We may now consider cases in which the contrasted characters of the two parents fuse or blend completely in the offspring. Cases of the sort are found not only between races, varieties, and elementary species, but this method of union has long been supposed to be a characteristic feature of hybridization when Linnæan species are crossed.

The most familiar and striking case of fusion or blending of two characters is found in the mulatto — the result of union of a white and a black individual. The mulatto breeds true in all successive generations, neither the white nor the negro ever appearing again in the pure form. If the mulatto again crosses with the white stock, the dark color is again lessened, but even after several generations of crossing with the white stock traces of the dark pigment remain. Conversely crosses between the mulatto and the black race produce ever increasing shades of darkness in successive generations of offspring. Not only the color, but the character of the hair also shows a tendency to blend in the hybrid.

Flourens made crosses between the domestic dog and jackal, the latter being, however, "prepotent." The horse and the ass give the mule, that is intermediate in many respects, but the

characters of the ass are more prepotent. The lion has been crossed with the tiger and an intermediate hybrid produced. The brown bear, crossed with the polar bear, gave a mixing of colors with the head and neck white. Darwin states that the pheasant crossed with domestic fowls gives a hybrid, showing the pheasant characters "prepotent." Darwin describes a cross between the penguin variety of the common duck and the Egyptian goose that is intermediate in character.

Mosaic Inheritance

A mosaic character sometimes appears when differently colored individuals are mated. Each character appears in its pure form over certain regions. Thus when a gray and a white rat are crossed, individuals sometimes appear that are mosaics, but it is questionable in this case, and perhaps in all such cases, whether the results may not be due to a latent mosaic character coming to light. As has been pointed out, offspring of the same litter may be different, some being of a single color, others mosaic. Whether spotted or piebald, domesticated races — horses, cattle, dogs, cats, etc. — owe their origin to a cross between two uniformly but differently colored parents, or are themselves *sports* that breed true, or have been back-crossed, is an open question. In pigeons, as we have seen, the mosaic character of the offspring is apparent. The results are complicated, however, by the ancestral (latent) blue color appearing in parts of the body. The inheritance of the mosaic pattern in mice and guinea pigs has been already discussed.

Hybridization between Linnæan Species

Most wild species of animals and plants differ from each other in more than in a single character. In the great majority of cases it is perhaps not going too far to state that species differ in all their characters — in some parts more, in others less. As already pointed out this is due, on the mutation theory, to the

saltations having been in most cases more than a single one, and often in different directions.

Now it is almost a universal rule — with exceptions, however — that wild species are infertile when crossed with other wild species, the degree of infertility differing enormously in different species — from complete fecundity to complete sterility. It is also a general rule — again with exceptions — that the more widely different two species are the greater the difficulty in crossing them. When the species are so different that they are put into different genera, the *chance* of their crossing is small. If the species belong to different families, the chance of crossing is much smaller still; and if to different orders, there is scarcely any chance at all of their crossing. Crosses between the domestic horse and zebras of different species produce infertile hybrids. A jack-ass crossed with a mare (horse) gives a mule, which is sterile. Conversely, a she-ass crossed with a pony gives a hinny, also sterile. On the other hand, the American bison has been crossed with the wild ox of Europe and has produced a fertile hybrid. Similarly, the humped cattle of India crossed with the domesticated ox produces fertile offspring. Crosses between the common goose and the Chinese goose, which are very different species, give fertile hybrids. Simliarly, for the common duck and the pintail duck, and for different species of pheasants.[1] A cross between a fowl (a langshan cock) and the common guinea hen has been brought about, but the hybrid is sterile.[2]

In regard to the characters of these hybrids no general statement can be made. Sometimes the hybrids appear to be intermediate in one or more characters; sometimes the character of one or of the other parent predominates, and in still other cases the hybrid may have characters peculiar to itself. Latent characters may also be brought to the front by hybridizing, and these dormant characters seem sometimes to be characters that the ancestors of the species may be supposed to have possessed.

[1] The preceding cases are quoted from Ewart's "Penycuik Experiments," 1899.

[2] Guyer, M. F., *Science*, XXI, June, 1905.

De Vries has found that some of the elementary species of the evening primrose also show a certain degree of infertility when crossed; and there can be little doubt that infertility may begin with the appearance of elementary species, and increase in proportion to every new change in the germ that takes place. Whether infertility is a general rule for elementary species, may be questioned.

Many cases of crossing between wild species of animals and plants have been recorded as occurring in nature, and many more cases have been experimentally brought about, especially in plants, with wild forms kept under domestication. The results are different in different cases, but it is a generally accepted opinion that the species-cross is generally intermediate between the parents. This conclusion needs, perhaps, careful revision in the light of the results of recent years on crossing types that differ in only one character, where in many cases discontinuous inheritance is the rule. Darwin was so impressed with the difference in the results of crossing Linnæan species and sports that he concluded that wild species could not have arisen as sports, since the latter when crossed show discontinuous inheritance, while wild species give intermediate forms. Since Darwin's time our knowledge of the results of hybridizing has greatly increased, and his argument seems less conclusive, because, in the first place, a single mutation may show incipient infertility, as in de Vries's œnotheras; in the second place, because the results of crossing elementary varieties and elementary species with the parent forms or with each other do not always show discontinuous inheritance; thirdly, because wild species have undergone so many changes of different kinds that the results are too complicated for an analysis of single characters; and, fourthly, because discontinuous inheritance may sometimes occur between wild species, if unit characters, rather than the ensemble of characters is considered. It is the failure to recognize this last point that has probably led to an exaggerated idea of the difference between the inheritance of single variations and of complex variations that characterize Linnæan species.

Lang has studied the hybrids between the closely related species of Helix hortensis and Helix nemoralis. These species are very similar, and it has often been disputed whether they are separate "species." They differ principally in size, in the form of the peristome of the shell and in the color of the lip, in the form of the "dart" and in the finger-formed gland. The hybrids are infertile with each other. Within the limits of each of these species there are the same kind of varietal differences, and these, as pointed out in the previous chapter, dominate and recede in the first species-cross. It is not possible to test their further behavior, since the species-hybrid is infertile. In regard to other characters, Lang states that these also dominate and recede. The hybrids are not intermediate, but have the form of the peristome of H. hortensis and the pigmentation of the lip and of the throat of the shell of H. nemoralis. The dart and the finger-shaped gland are exactly those of H. hortensis. Here it is evident that the hybrids are mixed, but that in some characters they are true to one species and in others to the other species. If the numbers of such characters were larger, the hybrid might appear to be a blend of the different characters, while in reality it might be only a mixture of one and the other parental characters. It is evident that the characters must be studied separately in such cases before we can conclude whether species-hybrids show blending of the parental characters or whether they give mixtures (mosaics) in their characters. Some characters may blend, others alternate in their inheritance.[1]

Dimorphism

The word "dimorphism" is sometimes used for cases in which the male and female differ markedly in form, but it is also used for those cases in which two forms of the same sex exist. I shall use the term here in the latter sense. Few cases of this sort exist amongst animals, and no experiments have been made to test the inheritance. The male hercules beetles occur under two

[1] Correns has described similar results in plants.

forms, one with the other without horns. There is a large and a small form of earwig. Papilio glaucus has two forms of females, one yellow, the other black. The latter is found over the southern range of the species. "In this region both yellow and black forms have been reared from eggs produced by a single female."

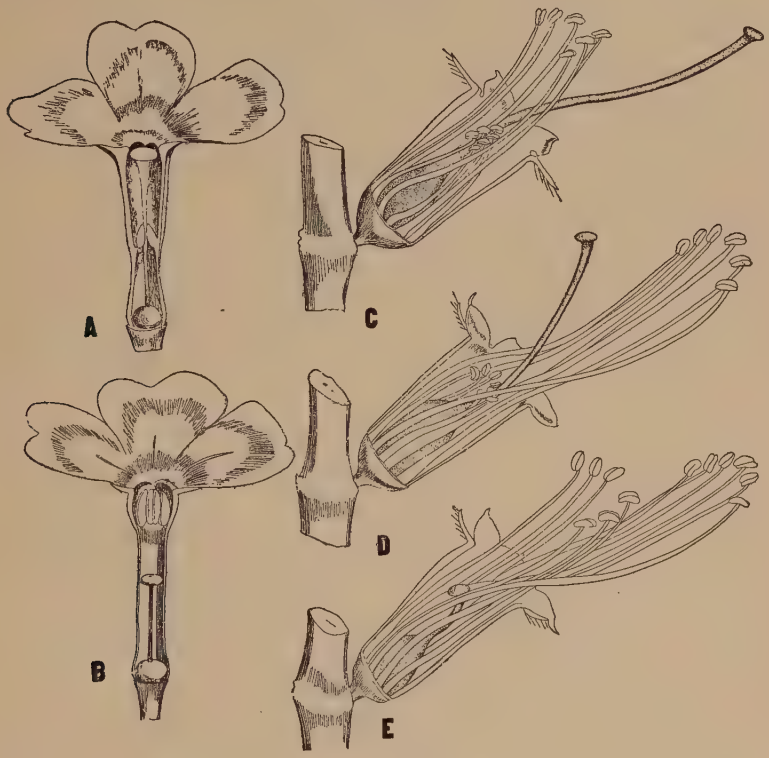

FIG. 17.

A number of cases are known in the higher plants, and their inheritance has been examined in a few instances. These are all hermaphroditic forms in which two kinds of flowers — both producing ova and pollen — are present on the same or on different plants. The European cowslip, *Primula veris*, occurs in two forms, the long-styled and the short-styled (Fig. 17). Each plant bears flowers that belong to one type only; the two types

never appearing on the same plant. The long-styled, as its name implies, has a long style reaching to the top of the corolla; the corolla is larger, the stigma globular, the papillæ longer, and the pollen grains larger than those in the short-styled form. This long-styled form flowers first, on an average, but the short-style averages more seeds. The stamens are in the middle of the tube in the long-style form, and at the top of the tube in the short-style form.

Darwin carried out a series of important experiments on these plants. He calls *illegitimate unions* those in which long-styled flowers are fertilized by pollen from the same flower or from a similar flower of the same or of a different plant. Similarly for the short-styled form: legitimate unions are those between long-styled and short-styled flowers.

The behavior of the offspring from seeds of legitimate and illegitimate unions is most surprising. In one case[1] an illegitimate union between short-styled forms produced seeds that germinated so badly that only 14 plants were obtained, of which 9 were short-styled and 5 long-styled.

In another experiment the stigma of a long-styled flower was fertilized by the pollen of a long-styled flower. Three long-styled plants resulted. From these, in turn, self-fertilized, 53 long-styled offspring were obtained; from their seed 4 long-styled plants; from their seed 20 long-styled; and from their seed 8 long-styled and 2 *short-styled*.

In another plant, Lythrum salicaria, 3 forms occur: the long-styled, the mid-style, and the short-styled type. The stamens also occur under the same three lengths. Figure 17 shows the conditions of the three kinds of flowers.

There are 6 possible legitimate unions and 12 illegitimate ones. To test these two kinds of unions, legitimate and illegitimate, 18 distinct kinds of crosses must be made. The results of these experiments are shown in the following table:—

[1] "Different Forms of Flowers," p. 217.

Nature of Union	No. of Flowers Fertilized	No. of Capsules	Average No. of Seeds per Capsule	Average No. of Seeds per Flower Fertilized
The legitimate unions	75	56	96.39	71.89
The illegitimate unions	146	36	44.72	11.03

The fertility of the legitimate to the illegitimate was found to be as 100 to 33, judged by the flowers that produced capsules, and as 100 to 46, as judged by the average number of seeds. Darwin concluded that *only the pollen from the longest stamens can fully fertilize the longest pistil; only pollen from the mid-length stamens can fully fertilize the mid-length pistil, and only the shortest stamens can fully fertilize the shortest pistils.* The meaning of this difference is entirely obscure. It is of much interest to find a condition of this sort between individuals of the same species. It suggests a comparison with the infertility that exists between different species; but in point of fact the results are just the reverse, for, in the present case, it is the same kind of flowers that imperfectly fertilize each other, while the flowers having a different form are more fertile.

In the case of dimorphic or trimorphic plants Darwin makes a determined effort to show that selection of fluctuating variations has brought about the two kinds of flowers. This argument is so instructive that I shall give it in full.

Since heterostyled plants occur in fourteen different families of plants, it is probable, Darwin thinks, that this condition has been acquired independently in each family and "that it can be acquired without any great difficulty." The first step in the process he imagines to have been due to great variability in the length of the pistil and stamens. "As most plants are occasionally cross-fertilized by the aid of insects, we may assume that this was the case with our supposed varying plant but that it would have been beneficial to it to have been more regularly cross-fertilized." "This would have been better accomplished if the stigma and the stamens stood at the same line; but as the

stamens and pistils are supposed to have varied much in length, and to be still varying, it might well happen that they could be reduced much more easily through natural selection into two sets of different lengths in different individuals than all to the same length and level in all individuals."

Darwin points out that the mutual sterility of these plants could not have resulted from natural selection, and although he thinks that the difference in the length of the stamens and pistils has resulted from a process of natural selection, yet he admits that one of the most striking facts in the case is that the individuals have in consequence become partly sterile to half the other individuals in one case and to three fourths in the other. This conclusion in itself shows, it seems to me, how futile it is to apply the theory of selection of fluctuating variations to the process of evolution of these forms.

Bateson and Gregory have examined the inheritance of heterostylism in Primula and have found that the Mendelian rule is followed. In the case of P. sinensis, the short-styled is dominant over the long-styled form. When long-styled was crossed with long-styled — pure forms being used — all the offspring (F_1) were long-styled. When these were inbred again, only long-styled forms (F_2) were produced.

The short-styled plants that were obtained for experimental work proved to be heterozygous (DR). When these short-styled were crossed with short-styled forms, there were produced 26 short- and 10 long-styled — the Mendelian expectation being 3 : 1. Of these 26 short-styled forms some were pure dominants (DD) and others dominant-recessives (DR). The latter (DR) inbred gave short (24) and long (4). It was found that other combinations also conformed to the Mendelian expectation.[1]

Bateson and Gregory also examined the inheritance of a peculiar form of Primula sinensis known as equal-styled. The anthers are at the same level as in long-styled flowers, but the style is short and does not reach above the level of the anthers. The corolla has a central yellow flush extending over half of each

[1] A few departures difficult to explain were also met with.

petal. "The flush is transmitted independently of the length of the style or the size of the pollen grains, for it may be transferred to the true short-styled or 'thrum' type. But when the flush is developed in plants which by gametic composition would be long-styled, the style does not pass through the anthers and the equal-styled condition is produced. Why the development of the yellow flush in these flowers should entail the reduction of the style, we cannot in any way suggest."

The discovery, that Primula follows the same law of inheritance as do other discontinuous variations, some of which are known to have appeared suddenly, furnishes an argument in favor of the view that the dimorphism in Primula owes its origin to discontinuous variation. Compared with the involved argument by which Darwin attempts to show how natural selection has brought about the result, the mutation theory offers a much simpler and in my opinion a much more plausible interpretation.

Reversal of Symmetry

In some species of snails the spiral of the shell turns to the right, in other species to the left. Occasionally in a right-handed species an individual that is left-handed is found, and there can be little doubt that such a form may suddenly arise. It is a discontinuous variation, but whether it is a mutation is not so clear, since the result may be due to an accidental shifting of the blastomeres on each other at the time when the unsymmetrical mesoblast cell is laid down. Nevertheless, the fact that entire species are characterized by the right- or the left-handed condition indicates that the factor that produces the one or the other result may at times be impressed on or arise in the egg, and be inherited. There are also species in which some individuals are right-handed, others left-handed. Here both possibilities seem to exist in the egg; but whether this can be referred to alternating dominance and recession, or to purely local conditions that arise during segmentation, is unknown.

Somewhat similar conditions occur in the two kinds of chelæ of crabs, prawns, and other decapods; and perhaps the right-

handedness and left-handedness in man belongs to the same category. It is also known that in man all of the viscera may be in a reversed position, and the aortic arch also.

Lang has bred together some left-handed snails of the right-handed species, Helix pomatia. They produced only right-handed individuals. These were also inbred and produced only right-handed young. It is evident that this new character is not inherited in this instance and also that it does not behave as a recessive to the right-handed condition, for, if it did so, it would have reappeared in the grandchildren.

Physical difficulties seem to interfere with the union of the sinestral individuals of Helix with dextral forms, so that as a rule the sinestrals are precluded from breeding, unless by chance they meet one of their own kind; but even if this occurs all the offspring will be dextral again, and no opportunity exists to perpetuate the new race. If, however, in other species the left-handed condition should be heritable, such individuals might, if once started, establish a variety alongside of the parent forms, although the two forms might be prevented by their difference in structure from pairing. That the left-handed condition must sometimes be inherited is shown by the existence of species of this sort.

Conclusions regarding Mendelian Inheritance

The examples of discontinuous inheritance given in the preceding chapters make it clear that Mendel's law accounts in many cases for the results, and is therefore an invaluable acquisition to our method of interpretation; yet in some other cases it is evident that the inheritance is not strictly Mendelian.[1] Used with discretion the law may still unlock many problems, but if attempts are made to force it to interpret cases that do not belong to its proper field of action, especially in regard to dissociation in the germ-cells, harm rather than good may temporarily result.

[1] The most striking exceptions are those recorded by Standfuss and by de Vries (œnothera). Other cases involve blending, etc.

The Mendelian inheritance of coat color in mice and in some other animals may give an exaggerated idea of the inheritance of color in general. That the inheritance is not always of this sort seems to be shown by a number of cases, some of which have been given. Pearson's examination of the inheritance of color in the coat of dogs, horses, and of the eye color in man, has led him to conclude that in these cases there is no evidence of Mendelian inheritance. He points out that when the whole range of the ancestry is examined we get more nearly an idea of what the color of the offspring will be. For example, in one case, where the color of the eye of the mother and of the father was blue, only two of the children had blue eyes; but in another case, where the father and the mother and all four of the grandparents and five recorded grandparents had blue eyes, four children had blue eyes. Single cases of this kind in themselves do not show much, but these are only samples of what is generally found in many cases of the sort. Pearson thinks that the prediction of what the color of the eyes is likely to be will be closer when we use the ancestry and not the parents alone. If any of these eye colors follow the Mendelian rule of dominance and recession, some evidence of this would appear in the statistics, but nothing of the sort has been found.[1] It is evident, nevertheless, that these cases require careful reëxamination, since there has probably been great intermingling of different colors in the past.

De Vries and some other students of mutation have laid much stress upon the immutability of unit characters. De Vries assumes that transitions between unit characters exist as little as between the molecules of chemistry. It cannot be maintained, I think, from the evidence that we possess, that unit characters are immutable, for there are some cases in which it appears that the unit character may be halved by every crossing. It is true that some of these cases may be explained by antagonistic characters both developing and mutually influencing the result; but if they do not subsequently separate, it is impossible to tell whether or not a new unit character has been formed by combination.

[1] "The Law of Ancestral Heredity," *Biometrica*, II, 1903.

Cases of blended inheritance especially seem to come under this heading. But so long as we do not know definitely what occurs in these cases, it seems to me arbitrary to speak of unit characters as immutable and quite unnecessary to make this idea a cardinal point of the mutation theory. The behavior of certain characters in heredity shows that they do act as units, and it is a great convenience to deal with them as such, but unnecessary to push the matter so far as to hold that they are immutable. If unit characters can be halved, altered, added to, or changed in any way, their immutability does not seem to be an essential point of their characterization, and, as has been said, there is some evidence to indicate that such changes may take place. The idea of immutability is not likely to suggest itself when results of this kind are considered, but in cases where complete dominance of one form over the other occurs, the idea of unit characters is more likely to arise. If, however, as I think probable, we are dealing here with alternate or contrasted characters that cannot both develop at the same time, the isolation of the characters in question is due to their mutual exclusion rather than to their immutability. Even if it be true that mutations take place by definite steps without the presence of intermediate forms, it does not necessarily follow that these steps may not subsequently become subdivided by each crossing with the parent form. The central idea of mutation remains, even if the unit-character that marks the steps is capable of being changed.

The results of hybridizing of forms differing by a single unit-character seem to show that when in the first generation the hybrids (F_1) are strictly like one of the two parents, the hybrids of the new generation (F_2) also show complete development[1] of one of the two characters in the extracted dominants and of the other in the extracted recessives. This may be called the law of incompatibility. If, on the other hand, the dominance is incomplete, *i.e.* if both dominate in the first generation, there is incomplete dominance in the second generation. This may be called the law of compatibility. If further facts establish these

[1] In the sense of contrast, not necessarily of actual separation.

laws as general, the results suggest certain questions of great theoretical importance.

For instance, the results seem to me to indicate that we are dealing not with a question of partial purity of the germ-cells, but with the question of the relation of dominance and recessiveness of contrasted characters. In the first generation there can be no doubt that both characters are present. In the first class of cases the activity of one character completely suppresses the activity of the other — the characters are mutually exclusive, *i.e.* the development of one suppresses the development of the other. In the second class of cases both characters may become active either at the same time in the same cell, producing blending; or in different parts of the soma, — different cells or groups of cells, — producing a mosaic or a piebald condition.

If, then, the same condition holds in the second generation, the most probable conclusion is, I think, that there has really been no separation of the contrasted characters in the germ-cells, but only a condition of relative dominance and latency established that is akin to but not identical with the dominance and recession in the first generation. Such a conclusion seems to me more in conformity with the results than that which tries to explain the facts of the second class as due to imperfect separation in the germ-cells of the two contrasted characters; for on my view the results in the first and second generation are accounted for on the same assumption; while in the current interpretation it is not apparent why imperfect separation in the germ-cell of F_1 should not occur as often in the first class of cases as in the second.

In the preceding pages the heredity of a large number of characters of domesticated animals has been described. Relatively few facts regarding wild species have been given. The objection has sometimes been raised that our domesticated animals are contaminated to such an extent by crossing that they offer questionable material for studies in heredity, and that the study of wild forms is more profitable. This objection is misleading, since it directs attention away from the point at issue and rests on several false or questionable assumptions.

In the first place, if we are to study those characters that behave, as a rule, as units, we can find for this purpose no better material than some of the domesticated races that differ from each other by single unit-characters. We are dealing here with the simplest cases of discontinuous variation, and the simpler the problem the better the opportunity to study it. In so far as the contamination due to previous hybridization is concerned there is introduced, it is true, a complication (but one that can be dealt with, in most cases), for the unit-characters, as such, are not necessarily affected by the latent characters, but can be studied independently of them. Hence it is not a serious difficulty to find that previous contamination has occurred. To ignore this point shows a misconception of the problem of the heredity of discontinuous variation.

It is important, in this connection, to bear in mind that the same rule of discontinuous heredity has been found to be true for wild forms also that differ from each other by a single character. Furthermore, how do we know that wild species are not also hybrids? If evolution has taken place by mutation, then it is possible that many wild species are complex hybrids, even if all of them are not. There will also be recalled in this same connection de Vries's conclusion that even his elementary species of Oenotheræ must also have arisen by hybridization, since it is improbable that a mutating germ-cell should meet another of its kind. Therefore, until it is more evident that wild species are not hybrids, this side of the argument carries little weight.

It is sometimes said also that wild species that have bred true for hundreds (or thousands) of generations are much purer than our "pure" domesticated races that have been bred for a relatively small number of generations. This may be true, provided it can be shown that a hybrid is purer the longer it is inbred. There is little direct evidence that this is the case, but the statement is likely to pass unchallenged because it seems so plausible!

Finally, if evolution has taken place by single steps, our first problem is to study the heredity and results of crossing of these single steps. Most wild species must differ from each other by

a large number of steps, and the results of hybridization of such forms may differ from the results of hybridization of single steps. If new elementary species arise by single steps and are subjected to crossing with the parent type, as would almost inevitably take place in many cases, the problem of paramount importance, from the point of view of evolution, is to study the results of such hybridization. Crosses between already established species are infrequent in nature and seem only in rare cases to give rise to new species, hence their study is of secondary importance from the standpoint of evolution, provided always that evolution has taken place discontinuously. On the other hand, it is unfortunate in many ways to attempt to estimate the value of the study of unit characters by the supposed bearing of the results on the theory of evolution; for while those who *believe* that evolution has taken place by simple discontinuous steps will ascribe the highest value to studies of this kind, those who *believe* that evolution has taken place in some other way will be likely to underrate the importance of the results as a contribution to the theory of heredity. Already the bitter controversies that the publication of these results has aroused are less concerned with the results themselves, that are accepted by all, than with the imagined bearing of the results on the theory of evolution. The intolerance that each side sees in the other is due not to the acceptance or denial of the results of the experimental work, but to the arguments that pretend to show that evolution has or has not taken place by discontinuous variation. Meanwhile there is danger that we forget the importance of the experimental results as a contribution to the study of heredity, whatever their bearing on the theory of organic evolution may be.

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CHAPTER XI

BEHAVIOR OF THE GERM-CELLS IN CROSS-FERTILIZATION

In the preceding chapters the characters of the hybrids resulting from cross-fertilization have been considered. The present chapter will deal with the behavior of the germ-cells themselves when cross-fertilization is attempted. In certain respects this topic covers a wider field than the preceding, since there are many more species in which the eggs may be entered by the spermatozoa of other species (and the early development take place) than of those that produce adult hybrids.

Experiments with Amphibia

Different species of European frogs have been frequently utilized in crossing experiments. The most important results are those of Rusconi (1840), Lataste (1878), Pflüger (1882), Born (1883), and Heron-Royer (1883).

It has been found in a number of different forms that the spermatozoa of one species will enter the eggs of other species and start the development. The egg may cleave, generally quite irregularly, but later stages than this may not develop. In some combinations the early, or even the later, gastrula stages may develop, but the embryos perish without going farther. Finally, in a few cases tadpoles, often having a weak constitution, may be formed. Thus the two closely similar species, Rana fusca (♂) and Rana arvalis (♀), cross readily, and tadpoles have been reared as far as the frog stage. The reverse cross gave no results. Bufo variabilis and Bufo cinereus also cross, and toads may be produced. The different races of Rana fusca intercross as readily with each other, as each race fertilizes its own eggs.

The other extreme is found where the eggs of Rana fusca are fertilized by the eggs of the salamander, Triton, and divide irregularly, but go no farther.

Pflüger concluded from his results that cross-fertilization depends less on the similarity of the adults than on the peculiarities of the spermatozoa. Thus the spermatozoa of Rana fusca and Rana arvalis are very different, and while cross-fertilization takes place in one direction it does not in the other. On the other hand the spermatozoa of Bufo cinereus and B. variabilis are much alike, and reciprocal cross-fertilization is successful. In support of his view Pflüger points out that the spermatozoa are most successful in crossing that have the thinnest or most pointed heads. Furthermore those eggs are most easily crossed that belong to species whose spermatozoa have the largest heads, because, being as it were so constructed as to admit their own large-headed spermatozoa, they do not exclude spermatozoa of smaller size. This view of the matter may explain the power of certain kinds of spermatozoa to enter the eggs of other species, but it does not explain why, after entering, certain combinations develop normally and others scarcely at all.

The conditions for normal development appear to be most readily fulfilled when the two species are like each other in structure, which usually, though not invariably, means consanguinity. Pflüger found that the eggs of the frog have the greatest power of being cross-fertilized at the height of the breeding season. Certain experiments that I have made on other forms indicate that this result may be due not so much to the eggs as to the greater mobility of the spermatozoa at this time. Hertwig has questioned Pflüger's conclusion, basing his objection on the evidence derived from some experiments that he carried out on the eggs of the sea urchin. He found that eggs could be more easily crossed when overripe or stale, as when they have stood for some hours in sea water, or after they have been injured by poisons. It has been shown more recently by Vernon that while in a few cases (*i.e.* in some species) more eggs can be cross-fertilized if they have stood twelve to twenty-four hours in sea water, yet in

most cases this does not hold. Eggs lose, as a rule, rather than gain in their responsiveness to foreign sperm if kept too long.

Experiments with Echinoderms

A number of investigators have made crosses between different species of sea urchins with varying success. In recent years Vernon, Boveri, Seeliger, Morgan, Driesch, Herbst, Loeb, and Godlewski have carried out experiments with these forms. Vernon found that out of sixty-four possible combinations, forty-nine gave the following results: twenty-nine developed to the pluteus stage, nine to the segmentation, blastula, or gastrula stages, and in eleven fertilization did not take place.

Vernon tried to show that the characters of the hybrid embryo are dependent upon the relative ripeness of the eggs and of the sperm in the two species that are crossed. He carried out his experiments with several species of sea urchins found in the Mediterranean. The breeding period of these animals extends over several months, or even in one species throughout most of the year. The height of the breeding season may be different for different species. During the time preceding and following that of the full maturity of the eggs and sperm, the eggs may still be fertilized, although fewer of them develop normally. For example:—the eggs of Strongylocentrotus reach their optimum in December or January, their minimum in July or August. Sphærechinus gives throughout the year mature eggs and sperm, although in summer the percentage of larvæ that develop is smaller. If the eggs of Sphærechinus are fertilized by sperm of Strongylocentrotus during the summer months, May, June, July, the hybrid larvæ resemble the Sphærechinus type (the mother), although some of them ($\frac{1}{3}$ or less) show traces of the paternal (Strongylocentrotus) type of larvæ. In November the hybrids approach more nearly the type of Strongylocentrotus (the father), and in December are entirely of this paternal type. In other words, as the sperm of Strongylocentrotus becomes more and more mature, it transmits to the larvæ its own characters.

The reciprocal cross, Strongylocentrotus ♀ and Sphærechinus ♂ gave less striking results, because of the greater difficulty in making the cross. In April, May, June, young stages were obtained that died. In July and August 29 per cent reached the pluteus stage. The hybrids showed no indication of their double origin, but were pure Strongylocentrotus (maternal). In November and December no eggs cross-fertilized.

Doncaster has carried out experiments in hybridizing sea urchins that lead him to conclude that the different hybrids obtained by Vernon at different times of year owe their peculiarities to the temperature of the water in which they develop. Herbst has recently carried out a more elaborate series of experiments that lead him to a similar conclusion, although he thinks that some other condition than temperature is also operative. What the other condition is he did not determine; but he does not think that it can be due to the relative condition of ripeness of the male sex cells. In fact, his analysis of Vernon's results, in the light of his own observations, seems to show, for the sperm at least, that Vernon's evidence is most unsatisfactory.

The preceding results apply more especially to the later larvæ or pluteus stages. In some respects the results seem to be inconsistent with results that other observers have obtained with the younger stages of these hybrids. Driesch has found, for instance, that the method of cleavage, its tempo, the character of the mesenchyme formation, and of gastrulation are characteristic of the egg irrespective of the kind of sperm that is used. In later stages, when the skeleton develops and the pigment appears, the larvæ first begin to show their hybrid origin. On the other hand, Boveri thinks that the hybrid characters appear very early, but the principal difference between his view and that of Driesch lies in the age at which each supposes the differences to become apparent. There can be little doubt, however, that, as a rule, in the early stages little or no trace of the paternal elements appear, and only later do they influence the characters of the hybrid. This difference may be interpreted to mean that, at first, the elements introduced by the sperm — the nucleus or

the cytoplasm — have not had time to act or to increase sufficiently in amount to affect the development. Most embryologists seem inclined to ascribe the effects entirely to the nucleus, which they believe dominates all the changes in the protoplasm. On the contrary, I am inclined to think that it has not been shown conclusively that this influence is nuclear in origin, but may possibly be due to the protoplasm introduced with the sperm. The slow increase in amount of the introduced protoplasm might account for the insignificant part it plays during the early development, when it is very small in amount compared to that of the egg-protoplasm. If, as others suppose, the chromatin of the nucleus is the all-controlling influence, it is difficult to see why this is not apparent at once, since the nucleus of the hybrid has equal amounts of paternal and maternal material. It may be fairly claimed, however, that the introduced sperm-nucleus requires time to change the protoplasm into its own sort of material.

The most striking case of the lack of influence of the sperm nucleus on the egg is that recently given by Godlewski. By following Loeb's method and making the sea-water alkaline, he has succeeded in fertilizing the egg of the sea urchin (Echinus and others) with the sperm of the crinoid (Antedon). The hybrids were of the sea-urchin type in all respects observed, including the pluteus stage.

Boveri carried out the ingenious experiment of fertilizing a non-nucleated piece of the egg of one species of sea urchin with a spermatozoön of another species.[1] The pluteus obtained was purely paternal. He concluded that the result was due to the introduced nucleus. Both Seeliger and I have taken exception to Boveri's evidence on the ground that the hybrid pluteus that can be obtained from nucleated pieces or from entire eggs is too variable in its characters to give support to Boveri's conclusion. In fact, some of these hybrids are so similar to the paternal type that they cannot be distinguished from it. Godlewski's

[1] O. and R. Hertwig had previously shown that pieces of the sea urchin's egg without a nucleus may be entered by spermatozoa of the same species.

experiment, described above, in which he used a non-nucleated piece of the sea urchin's egg and the spermatozoa of the crinoid produced larvæ entirely of the maternal type, which is the converse of Boveri's result.

Factors involved in the Entrance of the Spermatozoön

The entrance of a foreign spermatozoön into an egg is closely connected with the question of normal fertilization. What brings the sperm and egg together? How does the sperm enter the normal egg, and what delays or prevents its entrance into eggs of another species? The immense collections of sperm around the egg in normal fertilization has led to the idea that the egg attracts the sperm. Certain experiments seemed to support this view. Pfeffer's experiments with the antherozoids of ferns have often been cited as an instance of such an attraction. He found that when a dilute solution of malic acid was inclosed in open capillary tubes, and these tubes were immersed in a drop of water containing antherozoids, the latter collected around the open ends of the tubes, as though attracted by the malic acid. The evidence in favor of this interpretation has recently been considerably weakened by Jenning's study of the behavior of protozoa. These also will collect in a drop of acid, not, however, because they are attracted to the drop, but because no reaction takes place when they pass from water into a more acid solution. A reaction does occur, however, in passing from an acid region into water. The reaction involves a backing of the individual into the drop followed by a movement forward again in a new direction. On coming a second time to the edge of the acid area the reaction is again repeated. All individuals that pass by chance into the acid remain there — caught like rats in a trap — so that in time an accumulation occurs that might readily suggest that the animals had been attracted to this region.

Strasburger claimed that the eggs of the seaweed, Fucus, excrete a substance that attracts the spermatozoön from a distance of two diameters of the egg, but Bordet and Buller have failed to corroborate this observation.

Buller's experiments with the eggs of sea urchins and starfish have given important results. He pointed out that spermatozoa accumulate around immature eggs, and also around mature eggs that had been killed in osmic acid and then thoroughly washed in sea water. In this case it is highly improbable that any attraction could exist. The results are due to those spermatozoa that accidentally run into the membrane of the egg, remaining sticking there as a result of some physical property of the jelly or of some reaction on the part of the spermatozoön. Buller showed by means of the following experiment that the eggs do not secrete an attracting substance. Eggs were allowed to stand in a little water from two to twelve hours. Capillary tubes were then filled with this water and placed in a drop of sea water containing the sperm. No collecting of spermatozoa around the ends of the tube was observed. He alse tried other substances in the tubes, viz. salts, sugars, ferments, and alcohol, etc., but no evidence of their action in attracting the spermatozoa was observed.

Buller thinks that the spermatozoa are sensitive to contact, hence on coming into contact with the membrane bore into it. The spermatozoa swim in spirals in the water, but on entering the jelly they take a straight course, which in most cases will bring them into contact with the egg, although, if they should enter quite obliquely they may bore through the periphery of the membrane and pass out again on the other side. Thus even after entering the membrane, there is no evidence that the egg attracts the spermatozoa toward itself.

On the other hand it has been shown by von Dungern that the egg and its membranes may contain and even give off substances that act in some cases injuriously on the spermatozoa of other species. The egg of the starfish, Asterias glacialis, contains a substance that acts as a poison on the spermatozoa of the sea urchins — Echinus or Sphærechinus. The minimal lethal dose for sperm mixed with two cubic centimeters of sea water varies with different individuals between the limits of $\frac{1}{800}$ to $\frac{1}{6400}$ parts for half an hour. The same poison is found also in the skin of the starfish. Cross-fertilization of the eggs of this starfish by

sea urchin's sperm is thus prevented by the action of the poison, but it is going beyond the evidence to extend this conclusion, as has been done, to other starfish and other sea urchins without further examination.

In the sea urchin, Sphærechinus, there is a poison in the pedicellariæ that is injurious to the spermatozoa of the starfish, but if this poison exists also in the egg it is not strong enough to prevent the spermatozoön of the starfish from entering, at least in those species of sea urchins in which such a combination has been artificially brought about. The spermatozoa of Sphærechinus itself are killed by this same poison from its own pedicellariæ, but a much stronger dose is required.

It has been also found by von Dungern that extracts of the eggs of Echinus, Sphærechinus, Strongylocentrotus, or Arbacia do not kill the spermatozoa of the starfish even in the strongest solutions. Why, then, do not the spermatozoa of the starfish readily enter the eggs of these sea urchins? Their inability to enter appears to be due to another factor. The egg membrane of these sea urchins agglutinizes the spermatozoa of the starfish, *i.e.* they stick to it, and this interferes with their penetration. In Sphærechinus, however, agglutinization does not take place. Why, then, does not cross-fertilization occur here? Von Dungern claims to have found still another substance in this sea urchin's egg that excites even immature sperm to greater activity.[1] He believes that these exciting substances may in some cases prevent cross-fertilization because they change the kind of activity shown by the spermatozoa. He observed that spermatozoa that do not show rotational movement on meeting a solid, or semi-solid, body may do so when excited in this way and fail in consequence to penetrate.

Von Dungern also tries to show that eggs or egg membranes may contain substances that favor fertilization by its own sperm. Eggs of Echinus were rubbed up and mixed with pieces of jelly that had first been carefully washed. Spermatozoa were then

[1] Immature sperm excited in this way may then even fertilize their own kind of egg, *i.e.* starfish eggs.

added and observed to stand vertically to the surface of the jelly as they penetrated. If the piece of jelly was not first mixed with the extract, the spermatozoa simply rotated on its surface. On the other hand, starfish spermatozoa on coming into contact with Arbacia jelly behave as with the simple jelly alone, *i.e.* they do not stand vertically to it. The vertical position may be due, von Dungern thinks, to the presence of some substance in the extract that lowers the excitability of the spermatozoa to contact. Much still remains obscure, but these results show clearly some of the factors involved in fertilization and cross-fertilization.

Artificial Helps to Fertilization and to Cross-fertilization

A number of embryologists have found that normal fertilization may be assisted by adding certain substances to the water in which the sperm are placed. These substances excite the spermatozoa to greater activity, and in this or in other ways promote fertilization. It has also been known for a long time that the glands connected with the ducts of the male may secrete substances that make the spermatozoa active. For instance, Kölliker discovered that the secretion of the prostate glands of the male greatly excites the spermatozoa. Ordinarily the spermatozoa are quiescent as long as they remain in the testes or even in the ducts leading from them, but become active when the secretions are added or when set free in water. Roux states that the fertilization of the frog's egg is helped by the addition of one fourth per cent sodium chloride to the water, and Wilson has found that the spermatozoa of Patella can fertilize a much larger proportion of the eggs if a little potassium hydroxide is added to the sea water. Torelle and I have found that somewhat immature sperm of the starfish can be made active by ether, ammonia, salt solutions, etc., and will then fertilize the eggs. Von Dungern had previously observed that extracts of the eggs of the sea urchin excite immature spermatozoa to activity.

The most striking case of this sort is that of the fertilization of the sea-urchin egg by sperm of the starfish, recently described

by Loeb. If to 100 parts of an artificial sea water containing 0.3 cubic centimeter sodium hydroxide the eggs of Strongylocentrotus and the sperm of the starfish be added, as many as 50 to 80 per cent of the eggs will be fertilized. The eggs segment and it appears that even the early stage of development — more or less abnormal — may be reached.

Polyspermy

In the great majority of known cases only a single spermatozoön normally enters the egg to fertilize it. The moment one spermatozoön penetrates, some reaction takes place in the egg that prevents other spermatozoa from entering. The reaction involves, in some cases, contraction of the egg from the surrounding membrane; in other cases the formation of a membrane; and we may infer that other kinds of changes in the protoplasm may in other cases interfere or prevent the entrance of more than one spermatozoön. If the egg is injured or narcotized or is stale, more than one spermatozoön may enter. The result is generally injurious, for, while a regular or more often an irregular cleavage may follow, the embryo fails to develop properly. This failure seems to be due, in the main, to the unequal distribution of the chromatin or other materials to the different parts of the egg.

It has been found in hybridizing that in certain cases more than a single sperm enters the egg, and the irregularities in cleavage that follow seem to be due in part to this condition, but in other cases where one spermatozoön enters, the failure to develop must be ascribed to different causes. In these cases the results may be due sometimes to irregularities in the mechanism of division, but at other times to some incompatibility or failure of the two uniting elements to work together to a common end.

According to the degree of perfection to which the distribution of the materials of the egg is carried out, the subsequent development is more or less perfect. Even in cases where the hybrid reaches the adult condition, it has been observed that it may have a weak constitution, and even when it is strong the hybrid is

sometimes sterile. This sterility is due apparently, in some cases at least, to irregularities in the division of the germ-cells. When we recall that at one stage in the development of the germ-cells there may be a pairing and subsequent fusion of the maternal and paternal chromosomes, we can readily imagine that any differences in their behavior at this time might lead to disastrous results.

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CHAPTER XII

INBREEDING

For species with separate sexes the term "inbreeding" is used to express either the union between brothers and sisters or between offspring and parent, in one or more generations. It would have been convenient to apply the word "interbreeding" to unions between individuals of the same species — individuals not standing in close filial relationship — and to contrast this process with "cross-breeding" (or crossing or hybridizing) where the union is between different races, varieties, or species. Convenient as these distinctions might be, they have not been adhered to by writers, and the term "interbreeding" is sometimes used where inbreeding seems the preferable term.[1]

It is a general belief amongst breeders that inbreeding leads to injurious results. If this statement is intended to apply to all living species of animals and plants it is probably not true, but that it may be true in certain cases seems fairly well authenticated. Even in these latter cases the question may fairly be raised whether the results may not be due, *in part at least*, to the similarity of the external conditions under which the individuals have been kept. In other words, there is some evidence to show that if the external conditions are different for different individuals, the injurious effects of inbreeding are lessened or disappear in some cases; and conversely the breeding of individuals of different descent if subjected to identical external conditions might show the same deleterious effects as those associated with

[1] Darwin often used interbreeding where inbreeding in the above sense is meant.

inbreeding. It must always be remembered that some hermaphroditic plants are nearly always self-fertilized without apparent injury. They seem to be adapted to this process, while other plants that are adapted for cross-fertilization may show injurious effects if too closely inbred.

Darwin has paid much attention to this question of inbreeding. He has dealt with it extensively in his book on "Animals and Plants under Domestication." His general position may be summed up in the following quotations: "The evil effects from close interbreeding are difficult to detect, for they accumulate slowly and differ much in degree in different species, whilst the good effects which almost invariably follow a cross are from the first manifest. It should, however, be clearly understood that the advantage of close interbreeding, as far as the retention of character is concerned, is indisputable, and often outweighs the evil of a slight loss of constitutional vigor."

"The consequences of close interbreeding carried on for too long a time are, as is generally believed, loss of size, constitutional vigor, and fertility, sometimes accompanied by a tendency to malformation." It is generally supposed that the evil effects do not appear for several generations. "On the other hand, the benefit from a cross, even when there has not been any very close interbreeding, is almost invariably at once conspicuous."

Darwin says "That any evil directly follows from the closest interbreeding has been denied by many persons; but rarely, by any practical breeder; and never, as far as I know, by one who has largely bred animals which propagate their kind quickly." Despite the fact that crossing interferes seriously with the results of the breeder who is trying to keep his strain pure, all breeders practically without exception make use of crossing from time to time to strengthen their stock. Darwin quotes numerous cases amongst domesticated animals to show that inbreeding is injurious. In several cases where the pedigree has been kept with care there is distinct evidence of injury.[1]

[1] For details see "Animals and Plants," Chap. XVII.

Experiments with Mice and Rats

Von Guaita[1] has made some experiments with mice that had been already inbred by Weismann for 29 generations. He inbred the animals through seven generations and found clear evidence of diminishing fertility. In the following table the total number of young, the number of litters, and the average young in a litter are given.

WEISMANN'S DATA

1 to 10 generation:	1345 young;	219 litters;	aveg. per litter 6.1
11 to 20 generation:	252 young;	62 litters;	aveg. per litter 5.6
21 to 29 generation:	124 young;	29 litters;	aveg. per litter 4.2

Von Guaita's data, beginning with the mice of the last generation of Weismann's stock, are as follows: —

1st and 2d generations	3.5
3d and 4th	3.6
5th and 6th	2.9

Comparing the first and the last averages, it is seen that there has been a reduction in fertility of about 30 per cent.

Ritzema Bos inbred rats for 30 generations. The family started with a female albino white rat, that was paired with a wild rat, and gave twelve young. A white male of different parentage was bred to seven of these offspring, but later no other foreign blood was introduced during the six years of the experiment. Parents were bred to offspring, and sisters to brothers. The average number of young per litter is shown in the following table: —

1887	1888	1889	1890	1891	1892
$7\frac{1}{2}$	$7\frac{1}{7}$	$7\frac{12}{17}$	$6\frac{21}{36}$	$4\frac{7}{12}$	$3\frac{1}{5}$

During the first 20 generations (in the first four years) there was scarcely any decline in the productiveness, as the table shows, but in the following ten generations there was a marked and sudden decline. The number of pairings that were sterile increased steadily as shown in the next table: —

[1] *Berichte der Naturforschenden Gesellschaft zu Freiburg.* 1900.

1887	1888	1889	1890	1891	1892
0	2.63	5.55	17.39	50	41.18

The young of later generations also died at a much greater rate, as shown in the following table: —

1887	1888	1889	1890	1891	1892
3.9	4.4	5.0	36.7	36.4	45.5

It is noticeable that the mortality rose suddenly at the same time (1891) that the number of young per litter decreased. Pairing between brother and sister was found to give poorer results than pairing of father and daughter, or mother and son. Thirty-six per cent of the pairs of siblings were infertile, but only 21.4 per cent of the unions between parent and child. Pairing of young of the same litter gave essentially the same result as pairing of young of different litters of the same parents.

The weights of the rats decreased during the time of the experiment. The maximum size of a full-grown male was 300 grams in 1891; in 1892 few individuals reached the weight of 275 grams; and after six years the weight had declined to 240 grams. Crampe, who inbred rats, found that they became diseased and abnormal after a time, but Ritzema Bos did not find this in his experiments. He thinks that Crampe must have begun with a diseased stock, which became more diseased as a result of the weakening induced by inbreeding.

In the case of man there are many customs, beliefs, and superstitions regarding the effects of close inbreeding. Races in widely different parts of the world have rules prohibiting marriages between relations. It would be interesting to know how such regulations have arisen, since, as Darwin points out, savages have no finer moral or social feelings to consider, and are not likely to have taken into account the effects on distant progeny; for it is admitted that if evil effects are produced they are not likely to appear before several generations have closely intermarried. The abhorrence of incest, that is so pronounced in most races, can scarcely be claimed to be an inherent instinct, as Darwin points out. The Hindus have developed to an equal

degree the abhorrence of defilement by contact with other castes or with certain animals.

George Darwin, who examined the question, as far as the statistics were known, found no clear evidence of any evil effects caused by close intermarriage, or at most the evil was very small in amount, and out of all proportion to the prejudice against consanguineous unions. One might easily offer a number of possible explanations of the basis for this feeling, but such speculations would have little scientific value in the present state of our knowledge.

Experiments with the Pomace Fly

The most extensive series of experiments on inbreeding that have been made in recent years are those of Castle and his pupils. They have used the fruit or pomace fly, Drosophila ampelophila, which can be easily kept in confinement, and will breed throughout the year in a warm place. The whole life-cycle may be completed in eleven or twelve days (egg three, larva three, pupa three days, and two days before the imago begins to lay eggs).

Brothers and sisters were paired in each generation. A pair of pupæ of the same parentage was put into each jar. If the flies proved to be of different sexes, they were left together; if of the same sex, they were rearranged. The larvæ left the fruit on which they had fed and pupated on the top or sides of the glass. They were collected and counted, and the productiveness of the pair calculated on this basis. Sometimes no eggs were produced, which was at times due to the sterility of the male, at other times of the female, as shown by pairing them with other individuals.

The longest, or A-series, was carried through 59 generations extending over three years. We can appreciate the extent of the series if we compare it with the time required to produce the same number of generations of mankind. If we allow three generations to a century, it would take 20 centuries to give 60 generations. In other words, a corresponding experiment on man would

have extended from the beginning of the Christian era to the present time. The productiveness of the fertile pairs is shown in the accompanying curve. It will be seen that the productiveness fell during the winter of 1903, rose during the spring, and culminated in the late summer. It fell again during the next autumn and winter, but rose again during the next summer. It fell again sharply in the next autumn, but rose rapidly during

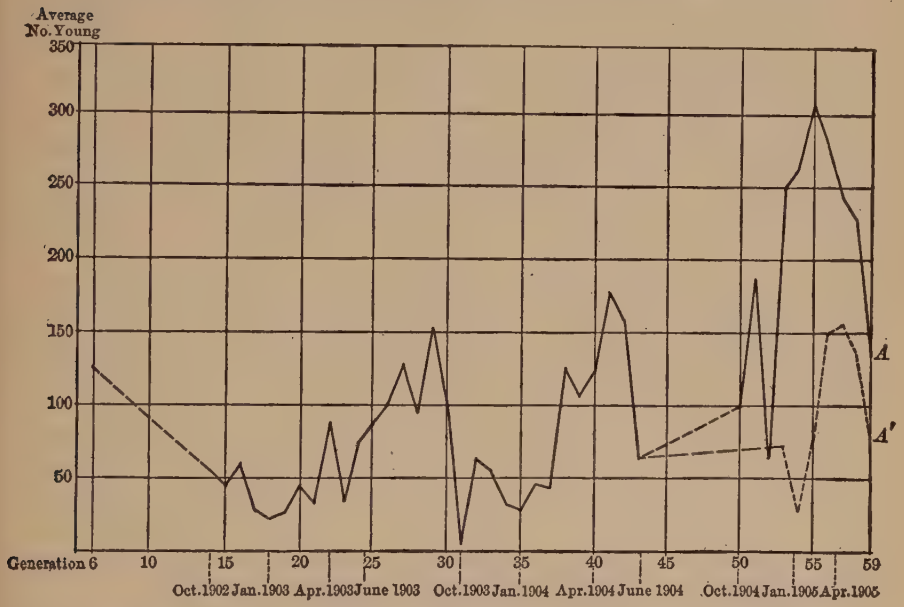

FIG. 18. Curve of productiveness of fertile pairs of A series of Pomace flies. (After Castle.)

the winter and spring, reaching a point much higher than at any previous time, but fell again during the spring. The last rise was connected with a transfer of the flies to a warm chamber.

This A-series is characterized by low productiveness, and an inclination to sterility, when compared with other series. The average number of young was never as high as 200 until the fifty-third generation, usually it was under 100, and about one in five pairs was sterile. "Control cultures made under identical conditions, but from stock not inbred, had a productiveness two or three

times as great and showed no signs of sterility." The productiveness of the A-series was not due to inbreeding, but was inherent in this stock from the beginning. That this is the explanation of the results is shown by comparing the A-series with other inbred series; and also by the sudden rise in productiveness of the A-series at the end of the third year.

Two other inbred series, M and N, were from the beginning more productive than the A-series. The average of eggs never fell below 200, except in a single generation, and was usually nearer 300, occasionally rising to 400 or more. The productiveness of this series, carried through 28 generations, is shown in the next diagram. No sterile individuals were found in the N-series and only one in the seventh, one in the tenth, and one in the fourteenth of the M-series. In the M-series "the average brood of the first inbred generation was 213, while the average for the series as a whole is 280, an apparent increase of fertility under inbreeding. In the N-series the first generation gave an average of 231 young, while the series as a whole gave 278.5 young to a brood." In both cases the first inbred generation may have happened to be lower than the average because of less skillful treatment. Hence a fairer comparison is between the first and the second half of the series, thus: —

	Generation 1–7	Generation 8–14
M-series	263	296
N-series	317	240

This comparison shows an increase in the productiveness in the M-series and a decrease in the N-series.

An interesting experiment consisted in crossing the M- and the N-series with the A-series. After crossing the two broods the offspring were mated *inter se* (brother and sister) for several generations in order to observe the effects on subsequent generations. The results showed that when a female of the A-series is mated with a male of the M- or N-series, her productiveness is not increased. The daughters, however, produce more young than

the mother and more than other A-mothers. Their productiveness is nearly the same as that of the M- and N-series. In other words, the male has transmitted the greater productiveness of his

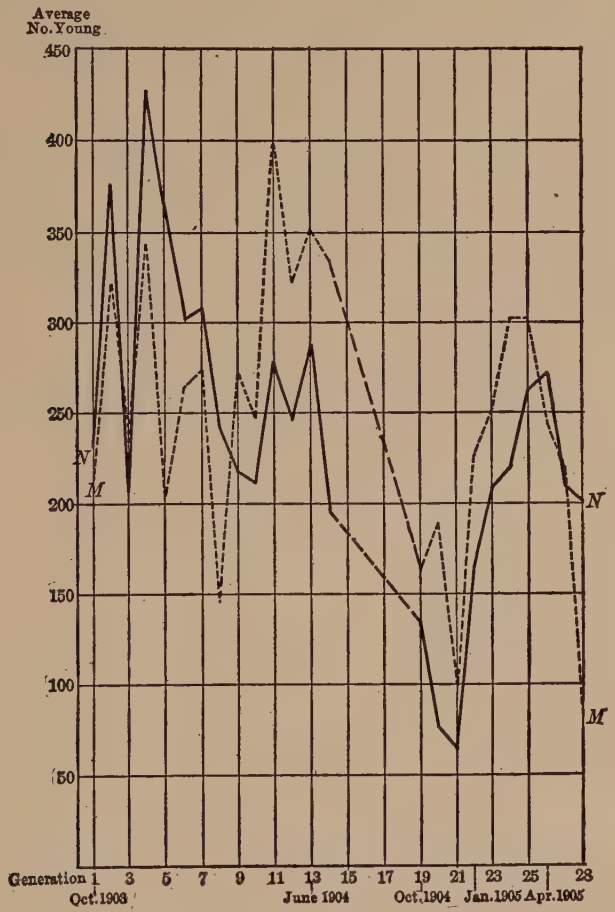

FIG. 19. Curve of productiveness of fertile pairs of M- and N-series of Pomace fly. (After Castle.)

race to his offspring. Complete sterility, however, appeared more often among the daughters than in the M- and N-series; and in this respect the influence of the A-series is observed.

Conversely, if a female of the M- or N-series is mated with a

male of the A-series, her productiveness is not decreased. In other words, the A-male produces enough sperm to fertilize more eggs than produced by the females of the A-series, and as much as needed for the M- or N-series. The difference in productiveness in the A- and the M- or N-series is due to a difference in the number of fertile eggs.

The daughters of this union showed the same productiveness as the mothers of the M- and N-series; but none were sterile. Productiveness, therefore, in both cases dominates less productiveness, unless, of course, the results are due to the cross itself bringing up the productiveness to the normal.

The grandchildren of both cross-series showed much variation in their productiveness. Some were as unproductive as the A-series and contained sterile individuals. Others are as productive as the M- or N-series. It appears that low productiveness may skip a generation and then reappear, as do characters that Mendelize.

Selection of individuals of the same brood, that show high or low productiveness, gives positive results. The pairs taken from more productive broods are invariably more productive, as shown by the following figures: —

	Parental Brood	Filial Brood
Lower productiveness	196	197
Higher productiveness	232	239

The annual cyclical rise and fall of productiveness, shown by the A-series in particular, but also by others, suggests the influence of external factors, especially when transference to a warm chamber increased at once the productiveness. The experiments show, in fact, that temperature, upon which proper fermentation of the food depends, has a distinct influence; but independently of this, some families are characterized by high productiveness, others by low. "Improved conditions increase the productiveness of all . . . but the response is more prompt and vigorous on the part of a race normally high in productiveness."

Castle's general conclusion is that "inbreeding probably reduces very slightly the productiveness of Drosophila, but the productiveness may be fully maintained under constant inbreeding (brother and sister) if selection is made from the more productive families. There are also indications that crossbreeding increases the productiveness of closely inbred families.

Behavior of Germ-cells in Inbreeding

Whether the decrease in fertility observed in some cases of inbreeding is due to the failure of the spermatozoa to enter the eggs, or to the failure of the fertilized eggs to develop, or to both factors, cannot be stated, but there are a few observations that show, indirectly, that the germ-cells themselves may be affected. These cases unfortunately apply only to hermaphroditic species.

It has been known to botanists for a long time that in certain flowers pollen will not fertilize the ovary of the same plant. In other cases where self-fertilization will occur, the pollen of other plants is prepotent over that of the same plant. It seems not improbable that the failure of the pollen to fertilize its own ovary is due to the failure of the pollen tube to grow down into its own stigma or style sufficiently far to reach the ovules. The prepotency of foreign pollen would be due on this view to more rapid growth than that of the pollen of the same plant.

Only one case of this sort is known in animals. Castle discovered that the spermatozoa of the hermaphrodite ascidian, Ciona intestinalis, fail, as a rule, to fertilize the eggs of the same individual, although they will fertilize the eggs of any other individual. I have carried out a series of experiments on this and other species in the hope of discovering to what this action is due. The results are complicated and difficult to interpret.

In the first place the sperm of an individual (Ciona intestinalis) does not fertilize equally well the eggs of all other individuals. In some cases 100 per cent of the eggs are fertilized; in others 25 per cent or less; but I have seen no clear case where the sperm in good condition is as sterile with eggs of any other individual as with its "own" eggs. The failure to fertilize properly is due

to inability to enter the egg, and not to failure of the developmental process after fertilization.

If the spermatozoön succeeds in entering, as it does in exceptional cases, the egg develops normally. It is possible by exciting the spermatozoa to unusual activity to cause them to enter the eggs of the same individual, and these develop. The failure, then, is due to the spermatozoa being unable to overcome some resistance met with in attempting to enter their "own" eggs. There is some evidence that the failure is due to something in the egg or its membrane that lessens the activity of its "own" spermatozoa that come into contact with it, or possibly to a failure of the egg to receive the proper stimulus to take in the spermatozoön; but if the latter, it is difficult to understand how exciting the sperm to greater activity should cause it to enter.

It is not possible to make the egg receive its own sperm by immersing it in the blood or extracts of the ovary of another individual. Conversely, it is not possible to make the sperm enter its "own" eggs by soaking it first in the blood or testis-extract of another individual. Allowing the eggs of an individual to stand for some time in sea water, so that any substance they excrete may be set free, and then placing the eggs and sperm of another individual in the same water, does not lead to self-fertilization. This experiment shows that the results are not due to soluble substances set free by the egg causing the egg to become fertilized by the sperm of another individual. Conversely, if the eggs of an individual are soaked for some time in sea water, and then sperm of the same individual is added in the same sea water and later the eggs of another individual are added, they will be fertilized. This result shows that the eggs do not set free a substance that brings to rest their own sperm, for, as shown in the experiment, the sperm will fertilize other eggs, if they are added to the solution. These and other experiments show that whatever the nature of the result, it is brought about by some insoluble substance in the egg, or is due to the failure of the egg to respond to the stimulus of its own

sperm, owing, perhaps, to the absence of some substance in the sperm. If, however, the sperm is excited to greater activity by alcohol, ammonia, ether, or by certain salts, it may force an entrance despite the resistance.

In another ascidian, Cynthia partita, I have found that self-fertilization often occurs, but the sperm generally fertilizes its own eggs less often than those of another individual. In the ascidian, Molgula manhattensis, self-fertilization occurs as readily as fertilization by sperm of another individual.

The failure to self-fertilize in some hermaphroditic organisms suggests that factors similar to those in Ciona may be at work in forms closely inbred for several generations, where the closely related males and females would seem to stand in somewhat the same relation to each other as the male and female generative organs in the same individual.

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CHAPTER XIII

INFLUENCE OF SELECTION

Artificial selection is par excellence an experimental process, and has been applied with success to all of the known forms of variation. It has been used in the case of *elementary varieties*, that follow the law of discontinuous variation and inheritance as described in the preceding chapters. Whenever, in these cases, Mendel's law holds, the formation of "pure" races can be quickly brought about by selecting the extracted dominants and extracted recessives. Where more than a single character is involved, the formation of a new race by selecting individuals containing two, three, or more desirable characters is more involved, and yet can be carried out with certainty. Selection produces nothing new in such cases, except in forming new combinations of already existing characters.

Selection may be applied to *elementary species*, which are new forms or sports that present one or more new characters. In this case isolation is the conserving principle of most importance; but in cases where a single individual alone comes into existence, it must be crossed with the parent type, and from the offspring obtained selection of those that have the new character must be made. If the new character is transmitted to all the offspring, no selection amongst them may be necessary; but if the new character follows the Mendelian law of splitting in the second generation, selection and isolation may be necessary to obtain as quickly as possible a new race. In this form of selection, also, nothing new is created, but what has appeared "spontaneously" is preserved.

The third form of selection is that applied to *fluctuating variations*. In the present chapter this topic especially will be

considered. It is a vital question for the theory of evolution whether new forms, new species, can be created by the selection of fluctuating or individual variations as the Darwinian school has claimed for nearly fifty years. Experiment alone can decide whether this claim is justified. That new forms have appeared as a result of selection by man no one will deny; for most of our domesticated animals and cultivated plants bear direct testimony in favor of this view; but the cardinal question remains whether elementary varieties and species, or fluctuating variations, have been intentionally or unintentionally picked out in the formation of new races.

Fluctuating or Individual Differences

Whatever systematic definition of species may prove most satisfactory, the fact that no two individuals are alike is what concerns us at present. I shall first give an account of the law followed by these fluctuations, then an account of their inheritance, and finally consider what man can accomplish by their selection and breeding.

Quetelet first drew attention to the law followed by fluctuating variations, and this law is spoken of as Quetelet's law. The fluctuations of animals and plants appear as though they were the outcome of chance, or, expressed differently, "the deviations from the average obey the law of probability." Let us take an example.[1] If we examine a group of men as to their height, we find by arranging them in a row that an almost continuous straight line will connect the tops of their heads. The line slopes from the tallest to the shortest man, but the slope is less inclined in the middle than at the ends. This means that there are in the middle region more men that are nearly the same height. In another way this important fact can be brought out more clearly. If we place in one column all the men between 64 and 65.9 inches; in another column to one side of the last all the taller men between 66 and 67.9 inches; in another column

[1] This example is taken from Davenport's paper, *Popular Science Monthly*, 1902.

on the other side all the shorter men between 62 and 63.9, and continue in this way until all the men are classified, we find a triangle-like group (Fig. 20, B). If we join the tops of the columns, we get a curve that corresponds in form to the mathematical curve of probability (Fig. 20, A).

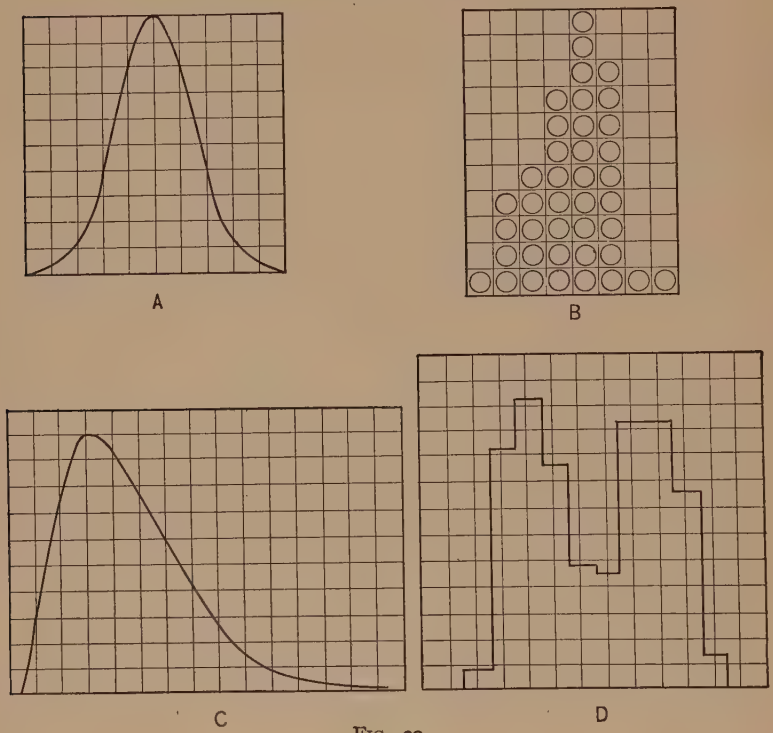

FIG. 20.

The same result may be shown graphically in another way. If we take a lot of peas and put all of a size (*i.e.* within certain limits) in similar cylindrical jars, and then arrange the jars so that the one with the medium-sized peas is in the middle, and those with the next larger peas on one side according to their size; and those with next smaller peas on the other side according to their size, etc., it will be found that the tops of the piles will give roughly the curve of probability. In both of these cases

the curve is given by the individuals themselves, but in practice this method is seldom employed. The measurements are used directly to construct the curve.

The causes of the differences in individuals are to be found partly in the various external conditions under which the individuals have developed, and partly in initial differences at the beginning of development in the individuals themselves. How far these latter may be traced to still earlier effects of external conditions, and how far to the possibilities of combinations of inherited differences within the organism itself is difficult to say.

It is clear that a knowledge of the curve of variability does not contribute, in any large measure, to an elucidation of the causes that bring about the fluctuations. These causes must be studied by examining the effects of the external factors that influence the organism.

If the curve of variability is high and does not extend out far along the base line, this indicates that the form is little variable. If the curve is low and extends far out at the sides, the variability is large in amount. One side of the curve is sometimes different from the other. Such a curve is asymmetrical (Fig. 20, C). Thus the curve may rise abruptly on one side and rise very slowly on the other side. The meaning of this is obscure. Equally important are the cases in which the curves have more than one summit. As an example, I may cite the case of the rhinoceros beetle (Fig. 20, D). Its curve has two summits. Such a curve is said to be bimodal. This means that there are many long-horned beetles and many short-horned ones, but few of the intermediate size. Here we see variations about two means, as though the group were about to split into two groups; but whether anything of the sort is really occurring is entirely unknown. It has been observed in certain plants that the secondary summits coincide with the points on which in allied species the main summit lies, and this appears to give us a suggestion concerning the factors producing the change. If, for example, we look upon the characters seen in the allied species as dormant in the one with two modes, but which may, under certain

conditions, be awakened to activity, we seem to get further insight into the conditions. That alternate or contrasted characters may exist in a single germ is well recognized. A further example will show the probability of this explanation. If individuals of two races, having different "modes," are crossed, the offspring will often show a tendency to give a curve with two summits — one for each parent mode. The characters of both parents are present in the offspring and sometimes one, sometimes the other, dominates. These, however, are special cases and are by no means to be taken to illustrate the usual effects produced by crossing two races.

Selection of Fluctuating Differences

We come now to the question of inheritance in regard to fluctuating variation. Ordinarily, succeeding generations show the same variations. This applies when the pairing of the individual is left to chance alone, and when the external conditions are similar. But the outcome is different if individuals showing the same kind of fluctuation are *picked out* or selected and inbred. The most striking results are produced, of course, when individuals showing one extreme or the other are utilized. Suppose, for example, we select two individuals, standing near the same outer limit of the curve — two individuals, let us say, showing the fluctuation in question developed almost to the greatest degree ever found. If the offspring of this pair be measured, it will be found, in most cases, that the average has been raised in the direction selected. The curve has moved toward the variation selected in the parents. In other words, and this is the important point, the average of the individuals is now higher than before, *i.e. there are now more individuals than in the preceding generation with the character in question better developed.* By selecting again individuals from the same extreme, the average can again be transferred in the same direction. As the process is continued, however, the average gain soon decreases, and finally stops without ever having transgressed the outer limit of fluctuation found in the first instance, provided

a sufficient number of individuals had been examined. It is true that these extreme individuals may be more common after careful selection through many generations, but the species cannot be carried as a whole beyond or much beyond the upper limit to which it sometimes attains without selection. Thus it appears impossible by the process of selection of fluctuating variations to transform the species into anything new or different from what it was.

There is a further point of especial importance in this connection. If vigorous selection of the extreme individuals is not carried out in every generation, there is a quick return to mediocrity, and what has been laboriously gained is quickly lost, — the species left to itself swings back to its more stable condition. The effects of selection are only temporary, and nothing permanent can be acquired in this way. Consequently we are justified, I think, in denying that through natural selection of individual differences the process of evolution could have taken place.

We cannot leave the subject without referring to Galton's important law of ancestral inheritance. This law states that each individual inherits *on the average* from his two parents together 50 per cent, or one half of the whole inheritance; from the four grandparents 25 per cent, or one fourth; from the eight great grand-parents one eighth of the whole, etc., the total inheritance being 100 per cent. It is probable that this rule[1] applies only to fluctuating variations, and not to cases of sudden or discontinuous variation to be discerned later.

Finally, correlated variation is often observed between different parts of the same individual, which vary together. For example, height in man is correlated with the length of the humerus. There are, however, other organs in man which do not seem to be correlated with height; for instance, the length of the clavicle.

[1] Pearson's law of inheritance is different (see Darbeshire), the correlation between successive generations being expressed by the fractions .3, .15, .075, .0375, etc.

Elimination within the Species

Although elaborate data have been published in respect to fluctuating variation and elimination within a given generation, comparatively few data have been gathered to show what occurs in successive generations under identical, as well as under different, conditions. Haphazard mating seems to produce the same variation in successive generations, despite the accidental elimination in each, hence in many cases nothing appears to be gained permanently by the elimination of the unsuccessful or of the unfortunate individuals. In order to discover to what extent the causes of fluctuating variation are internal and to what extent external, we need experiments carried out through several generations on pedigree animals, selectively paired, and kept under constant conditions. While such results may or may not throw light on the formation of new species, they will be of much importance as a contribution to the study of variation within the limits of the species.

The elimination of individuals within each generation may be due to catastrophes that overwhelm all the individuals involved, without regard to their individual differences, and the great destruction of immature individuals appears to belong largely to this class; or the elimination may follow the lines of individual differences which gives a selective value to the survivors. Which of these, or of other kinds of elimination, occur even for those forms that have been studied statistically, is known only incompletely in a few cases.

Weldon has measured the frontal breadth of Carcinus mænas, found living in the harbor of Plymouth. The measurements were made in the years 1893, 1895, 1898, and show, during this time, a decrease, which he believes to be due to elimination brought about by a change in the water of the sound. The mean of the frontal breadth for 1895 was less than for 1893, and a further change was found in 1898. These results are for male crabs. The changes in the female were less in amount. The elimination is due, Weldon thinks, to the fine mud, brought

down by the rivers that became greater in amount during these years. He tested this view by keeping crabs in water containing the same mud in suspension. The crabs that died were on the whole broader than those that survived. Weldon suggests that the frontal breadth is correlated with the breadth of the opening into the gill chamber, and the latter determines the amount of mud that enters, and in this way the elimination is produced.

Should these conclusions of Weldon be established, they show that a change in the external conditions may cause the elimination of certain individuals of the species, and in this way affect the mean of the survivors. In other words, natural selection occurs within the limits of the species. But it does not follow from this, as Weldon takes for granted, that if the same process of elimination were continued, a new species would be evolved. Raising the mean to the highest point attainable within the limits of the species does not necessarily lead to the formation of a new species. This point has already been discussed in other connections.

Crampton has studied variation and elimination in the moths of Philosamia Cynthia. In the first generation that he studied there was a high rate of mortality, and since the pupæ were collected in their normal environment, before they had been subjected to the winter frost, the death rate must have been connected with some inherent weakness or with conditions that they met with during their normal life. Out of 942 pupæ collected, there were 628 that were dead, so that only 329 "selected" individuals remained. The causes of the death of the 628 pupæ are not known. One might suspect that they had become parasitized; but Professor Crampton tells me that he examined them to see if this was the case, and found no evidence of the sort. It does not seem probable that the external conditions to which the pupæ were exposed had anything to do with the high death rate, and its causes are probably to be found in the organization of the animal. Whether bacterial disease, or disease of some other kind, is responsible for the results, was not

determined, but Crampton found no evidence that the death could be assigned to such causes.

Only 181 perfect moths (97 males, 84 females) emerged; 75 were imperfect to a slight degree, 38 were malformed, and 16 failed to metamorphose at all. It will be seen that only 16.6 per cent of the individuals that pupated became perfect adults.

Measurements of the pupæ show that the survivors are longer, narrower, and deeper than the eliminated pupæ. It also appears that survival does not necessarily or invariably accompany a condition of lower variability, although such a relation is generally observed. Crampton's general conclusion is that the elimination is based on the general and total efficiency of the individual, and "this is determined by the proper coördination of functional and structural elements. The actual basis for elimination is, in a word, 'correlation.' If this correlation is slight, the individual ranks as unfit; if it is higher, the individual is fit and more likely to survive." Whether the correlation itself determines the outcome, as Crampton appears to mean, or whether the lack of correlation is due to some deeper-lying imperfection, such, for example, as the presence of disease in the caterpillar which determines *both* the lack of correlation and the failure to develop, cannot be stated. If the latter is the case, the lack of correlation is only an index of a diseased or imperfect organization, and therefore not in itself responsible for the elimination. Crampton's idea, however, is that the imperfect correlation is due to formative factors in the insects themselves which leads directly to their death, and not to elimination due to external conditions.

Variation and Parthenogenesis

The problems of variation and of inheritance have generally been studied in animals that reproduce sexually. In only a few parthenogenetic forms, namely, in some insects, in aphids and in the honey bee, and in the crustacean, Daphnia, has the problem of variation been examined. Weismann advanced the idea that the *purpose* of sexual reproduction is to

induce variability. It is interesting, therefore, to find that variability may be as marked in non-sexual forms produced parthenogenetically as in sexually produced forms.

Warren has studied the variation of one of the aphids, Hyalopterus trirhodus, and of Daphnia. The aphids, to consider only this case, were inclosed in small bags on the leaves of their native plant, and the parents and their full-grown progeny were later killed and measured, the distance between the eyes and the antenna length being the two measurements taken. It was found that the external conditions, including also the natural changes in the food plant, produced very decided effects, especially in size, so that it was not possible to rear successive generations under identical conditions. Of 522 offspring registered, 455 grew up. The death rate for the second generation was 12.8. The larger mothers tended to produce healthier offspring. The variability of the second generation was found to be greater than that of the parents, and this is the rule also for sexually produced offspring — in man, for example. In the third generation the variability was diminished, attributed by Warren to the poorer external conditions, which, affecting the size, reduce the distance between the eyes more than they reduce the length of the antennæ. In general, the results show that the variability of a parthenogenetic race is not smaller than that of sexually produced forms. Casteel and Phillips have found in the hive bee that the males or drones that develop from unfertilized eggs are more variable than the females that come from the fertilized eggs.

The Results of Selection and Hybridization of Wild Elementary Species

Domesticated animals and plants in different countries often show differences other than those that can be attributed to differences in climate, etc. It has been stated that in some cases the domesticated forms bear a close resemblance to the local wild races of the country, or else show traces of such a similarity. The results may be due to man having brought under domestica-

tion the particular wild forms found in his vicinity. More often, however, the results may be due to the wild forms having been crossed with the domesticated forms so that the characters of the former have become impressed on the domesticated animals and plants.

There is satisfactory evidence in the case of plants to show that wild "varieties" and elementary species have often been crossed with domesticated plants in order to produce hybrids having one or more of the characters of the wild forms. Not only have wild varieties of the surrounding country been used, but wild varieties from all parts of the world, especially in modern times. Thus many of our domesticated animals and plants are hybrids, and the process of selection has been employed to pick out, amongst the great diversity of types produced in this way, those forms that have a practical value or that appeal to man's æsthetic or commercial taste, or to his fancy for novelties.

It is probable in many of these cases that the wild "varieties" that have yielded valuable results are true elementary species having fixed characters that have come from germinal variation, and not local races whose peculiarities are due solely to the external conditions to which they have been subjected.

Selection under Domestication of Mutations, Saltations, Sports, and Discontinuous Varieties in General

It is probable that the sudden occurrence of sports or saltations has furnished breeders with much of the material for the production of new forms. It has long been known that new types appear in domesticated animals and plants. If these are picked out — selected — and progeny raised from them, it is possible to establish a new race. In the case of hermaphroditic plants, self-fertilization of the new individual will give at once a large number of individuals like the parent. In unisexual animals and plants the new form must be crossed with the original stock from which it sprang. In some cases all of the offspring may be like the new form, and from some of them a new, fixed type may be raised. In other cases, all the offspring may be

like the old form, but, if interbred, some at least of their descendants will give the new race. Occasionally the new type bred back to the parent type may give a hybrid intermediate between the two parents, and this hybrid may become the parent of a new race that does not revert to either parent type. These different cases will later be considered more fully. For the present it will suffice to call attention to the fact that it is generally possible in one of these different ways to produce a new race by selection and isolation, and it appears probable that sudden variations of this kind have furnished the breeder with his most valuable material.

A point of great importance is that the new type may at first not differ very much from the original stock; and hence may often appear to be only a fluctuation. If, however, the new type reappears in the same strength in its offspring, it shows istelf to be a mutation and not a fluctuation. Until within quite recent years this distinction has not been fully appreciated, and all small differences were assumed to be fluctuations.

The origin of most of our domesticated forms is unknown; their history goes back to a remote time. Nevertheless within comparatively recent years a number of new types — sports or mutations — have arisen and their history is a matter of record. A relatively large number of such instances are known to botanists, and de Vries has recently given a careful analysis of such cases that appear to be authentic. Fewer cases are known to zoölogists; the more important of these may be briefly given.

The most remarkable instance is that of the ancon ram. There appeared in 1791 in a flock of ordinary sheep a ram with short legs and a long body. This ram, bred to a ewe of the common type, produced descendants having the same characteristics as the ancon father. In this way the new race originated which breeds true to the new type. The turnspit dog has short and crooked legs, recalling the condition of the ancon sheep. Darwin states that this kind of monstrosity is not uncommon in various animals, and cites the case of jaguars in Paraguay, and of a

pariah dog in India. It would seem that the result must be due to a single change of some sort in the germ that involves a correlated change in many parts at once.

The Mauchamp breed of sheep originated also from a single individual ram that appeared in 1828. The wool is long and straight, not frizzled as in the merino. The ram and his immediate descendants showed also other new structural characters. The individuals of this breed are "of small size with large heads, long necks, narrow chests, and long flanks." These peculiarities are removable by "judicious crosses and selection."

A monstrous breed of cattle exists in South America, the niata cattle, that must have originated from the introduced cattle; and to judge from its peculiarities, the breed must have appeared as a sport, although its actual origin is unknown. The upper lip is drawn back and the nostrils are situated high up. The exposed incisors give a peculiar appearance to these animals. The skull is much modified, the hind legs are shorter than usual, etc. The animals breed perfectly true to their kind. The short-horn cattle are also said to have originated from a sudden variation.

A most interesting case is that of the Japan peacock, or black-shouldered kind. This form has appeared several times in England and differs so much from the ordinary forms that have given birth to it that it would be ranked as a different species were not its parentage known. The birds breed true and have been known to replace in time the flock from which they arose.

Several other cases are on record. Sports have been recorded among domesticated fowls, pigeons, horses, mice (rhinoceros mice), and frequently in plants of many kinds. They are known to have furnished the basis for several domesticated races. Unfortunately exact information of the origin of races in this way would only be recorded when the saltation had been large in amount. When small, the change would be put down to fluctuating variations, especially by breeders who have had heretofore little interest in the difference between these two kinds of varia-

tion. The fact that so many of the domesticated races breed true furnishes the strongest evidence in favor of the view that they have originated as sports and not as the result of the selection of fluctuating individuals. In fact, as has been said, it appears that a race produced by selection of fluctuations can only be kept up by a rigorous process of selection, as shown in the cases of some cultivated grains, flowers, and beets. Most domesticated races, however, differ from these in one all-important respect. They do not need a process of selection to maintain them after they have appeared, and, as I have said, this is very strong, indirect evidence in favor of the view that they have arisen by the selection of sports or discontinuous varieties, whose chief peculiarity is that they transmit from their inception the new characters to their offspring.

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CHAPTER XIV

THE THEORY OF EVOLUTION

In the preceding chapters we have examined the evidence concerning the influence of external conditions in bringing about changes in the structure of animals; we have examined the claim that acquired characters are inherited; we have also studied the results from hybridizing in Mendelian and other cases, and we have considered the problems connected with the differences between the inheritance of fluctuating (or continuous) and of definite (or discontinuous) variations. The evidence from these different sources has unquestionably a very direct bearing on the problem of organic evolution, yet so many questions are still unsettled that any conclusion drawn from the evidence that we now possess must be provisional and perhaps premature. It is with this understanding that I venture on the following analysis of the bearing of the evidence on the theory of evolution. That the process of evolution is complex, and that many conditions and several kinds of variation may have contributed to it, most zoölogists seem at the present time willing to admit. If in the following pages I have laid especially emphasis on the results of recent experimental work on discontinuous variation and inheritance, it is because we have here, I think, the most satisfactory evidence in regard to certain factors that may have played an important rôle in the process of evolution. Other factors may also have been involved, but we have insufficient experimental evidence to prove that this is the case.

The formulation of the modern theory of evolution we owe chiefly to the French naturalists, Buffon, Lamarck, and Geoffroy St. Hilaire; to some extent also to Erasmus Darwin. Their theories were based largely on evidence from comparative

anatomy, embryology, and paleontology. Charles Darwin occupies a unique position. Like his predecessors, he argued for the theory of evolution on the basis of comparative anatomy and paleontology, but in addition he brought forward his theory of natural selection to account for the "origin of species," as the result of the survival of the individuals that are better adapted. In support of his theory of natural selection he introduced the evidence from artificial selection as carried out by man. Here almost for the first time the experimental study of evolution was begun. Darwin's more immediate followers, however, did not carry on the experimental work much beyond the stage at which he left it. In the last decade, however, great activity has begun along experimental lines with most promising results, and at the present time the study of evolution has passed into an experimental stage.

The results that de Vries has obtained with plants in his experimental garden have opened a new era in the study of evolution, for he has shown that the process may not be so slow that it can only be detected by elaborate mathematical calculations, or at least that it may at times be rapid and easily detected; and, what is more important, he has shown that this process is going on at the present time. De Vries's results will be described later, and his evidence compared with that obtained by zoölogists for animal forms; but before taking up de Vries's work, certain other considerations must first be dealt with.

The Analogy with Artificial Selection

If, as Darwin supposed, the domesticated races have been formed largely by the selection of fluctuating variations, a strong argument, at least, would have been established in favor of an analogous method in nature having produced wild species; but it is probable that Darwin relied too extensively on the statements of breeders and amateurs as to the process by which their results were obtained. It is clear that many of these breeders lack the scientific training and appreciation of the value of evidence to make their conclusions trustworthy, and however interesting

and suggestive their work may be, it needs to be carefully revised and verified before it is safe to build on it a theory of evolution.

In the case of artificial selection it now seems probable that selection of *definite* variations, the introduction of wild races, and the results of hybridizing have all played a far more important rôle than the selection of *fluctuating* variations. The evidence is clearer in the case of plants than in that of animals. In animals the domesticated races have been, in most cases, longer in confinement, and the history of the origin of the different forms is lost in the remote past. Nevertheless it is not probable that the method employed in producing domestic races of animals has been essentially different from that of plants; and in a few cases, at least, there is evidence that the same method has been employed for both.

The Influence of the Environment

Zoölogists and botanists alike have been impressed by the fact that under different external conditions different species are found. While this statement does not hold for all species, yet it holds for many. Natural barriers also are likely to separate different forms (races) of the same species, and isolation of any kind seems to be connected in some way with the occurrence of different forms.[1] It is not my purpose here to consider the different hypotheses that have been built up on this evidence, but the fact itself is so patent and so important for our present purpose that it must receive here somewhat fuller treatment.[2]

A not unnatural inference from the facts of distribution is that

[1] Gulick has recently (1905) gone over this ground exhaustively, and the influence of isolation has been discussed by a number of specialists, Jordan, Allen, Merriam, and others in recent numbers of *Science* (1905–1906).

[2] Isolation is often *assumed* to produce its results by preventing the new forms (however they may arise) from crossing back with the parent species, yet it is by no means true for all species and varieties that they are isolated from each other except in so far as their special conditions of life are different. Internal differences may produce physiological isolation which appears as potent a factor as geographical isolation. It might be confusing cause and effect to assume in the former case that the isolation produced the new forms. A new mutation may itself cause its own isolation.

external conditions have slowly modified the forms, and the evidence for this view seems almost irresistible when we find that many animals and plants are distinctly modified when placed in a different environment, without, in most cases, however, transcending the limits of the variety or race.[1] On the other hand, it is equally true that when brought back to the original environment the changed forms return in most cases to their former condition. In this respect they differ from wild species, from fixed varieties, and from elementary species, which remain true to their type under varying conditions, except for the temporary changes just mentioned. Therefore it does not seem probable that changes of this kind directly transformed one species into another. Suppose, however, that a new environment may sometimes call forth in the germ-cells effects that are *definite* and inherited, — fixed, in other words, in the sense that the germ-cells are true to their kind, — then we can perhaps harmonize the apparently contradictory evidence. The new mutation thus induced might be, in some forms and under certain conditions, similar in kind to the effects produced on the body-cells. The results, however, would not be reached *through* the body-cells, but by independent, definite variation of the germ-cells, as a result of a new environment. Offspring from such germ-cells should remain true to their new kind when returned to the original environment unless the germ-cells are again affected; but whether a return to the original type would even then occur cannot be stated. Macdougal has recently made the important discovery that mutations may be induced by treating the germ-cells of the evening primrose with salt solutions.

In other cases the new mutation or mutations may not be in the direction in which the body-cells are temporarily affected (if affected at all), but in some other direction or directions, and new types are formed bearing no relation to the former modifications affected in the body-cells. That the new type may also

[1] This statement is somewhat arbitrary. It is intended to mean that with a return of the former conditions the new type returns to its original condition.

have temporary effects produced in its somatic cells by the environment must be granted, but such effects should not be confused with these permanent mutations brought about in the germ-cells. On some such hypothesis as this it may be possible to harmonize current views.

De Vries's Results with Œnothera

Although de Vries's experiments have been made entirely with plants, the results are of so great importance that they must be stated here briefly; for there can be little doubt that if his conclusions are established they will apply equally well to animals. His principal work has been with Lamarck's evening primrose, Œnothera Lamarckiana. This American species has been introduced into Europe, where it has been cultivated in gardens for a long time. It has also escaped and established itself in a wild condition. De Vries found a field at Hilversam near Amsterdam in which the escaped evening primrose grew, but also several other closely related forms which as subsequent experiment showed had sprung from Lamarck's primrose. These new forms bred true, when self-fertilized, showing that they were fixed types and not local races depending on special conditions. They are new elementary species.

When the seeds of Lamarck's primrose were sown in de Vries's experimental garden, a small percentage of them gave rise to some of the same types that had been found growing wild. Other types also appeared. In all, de Vries has described seven such elementary forms. The chief character of these mutations is that they breed perfectly true to their type when self-fertilized. Occasionally another new type may appear from the seeds of a mutation itself. These also in most cases breed true to their kind if self-fertilized. The parent type, O. Lamarckiana, has been found to produce year after year its quota of mutations. The percentage of new forms, although small, — not much more than about 1.5 per cent, — seems to be constant, and the mutants continue to appear year after year.

De Vries has formulated a theory or rather several theories

based on these results. He lays much emphasis on what he calls *physiological units* or unit-characters, but disclaims any desire to locate these in any special part of the cell, and believes the evidence justifies him in supposing that each new step or mutation involves a change in the organization of the germ-cell of such a kind that a new unit-character appears. The change may be slight or great compared with the parent form, but its unity is shown by its behavior in heredity. New elementary species are characterized by having at least one new physiological unit. By way of example I may cite the following cases of mutations amongst animals. The appearance of the merino ram was probably due to some physiological change in a germ-cell of one of its parents of such a sort that one character especially, viz. the wool, was changed. Other less striking characters were also present, and inasmuch as these are always associated with the merino type of hair, they all belong together. The ancon ram showed differences in the proportion of nearly the whole body; but the entire change must probably be referred to a single, although profound, unit change in the germ-cells. The occasional appearance of the turnspit type of dog, which resembles the ancon ram in the form of its body, indicates, if it does not prove, that this kind of change, involving nearly all the parts of the body, may readily occur. So numerous are the parts affected in these cases that it is impossible to ascribe the results to "accidental" combinations of the different organ elements, for it is inconceivable that just these combinations could ever appear more than once, but must be due to some definite change in the germ-cells which can appear in this particular way. The same statement must also hold for Lamarck's primrose, where, however, instead of one possible combination there are several possible ones that become realized. If we use Galton's oft-quoted comparison of a polyhedron, we can see that resting on its most stable face it may be rocked back and forth, but always returns to its same resting-place. Such oscillations on a single face would correspond to the fluctuating variations of a species. Should a greater movement take place, the

polyhedron may roll over on to another face, which would correspond to the change of a species into a new one. Should the polyhedron be so constructed that one of the new faces is much more stable, or easily reached, we can understand why in some cases only a single mutation is likely to occur when the balance is upset. Such would be the case with the turnspit type of dog, the Japanese peacock, the merino sheep, the short-horned cattle. If, on the other hand, one new face is as likely as the other to give a stable condition, results like those in the primroses would seem to be produced. We might even go farther and conclude that this has been the case with the two hundred elementary species of Draba verna, with the many elementary species of the wild apple, and possibly with the races of domesticated pigeons. The analogy need not be pushed too far, nor be taken for more than it is worth.

De Vries attempts to draw a sharp line between elementary species and varieties, and while the distinction is useful, yet, on the whole, it seems rather arbitrary. A variety is a type in which one of the parent-species characters has disappeared — not necessarily absolutely, for it may remain only latent in the germ-cells, but it never develops or only under unusual conditions.[1] As an example, an albino mouse is a variety of the house mouse. It is characterized by the loss of a character — the pigment. Nevertheless as we have seen in the preceding chapters the character that disappears may really be only latent in the germ-cells.

It is evident that it may often be convenient to distinguish between new types in which a new character or combination of characters has appeared, and new types distinguished only by the loss of a character. The distinction may seem to be one of only minor importance were it not that it has been held to separate new types that obey quite different laws of heredity. It is sometimes said that varieties, in de Vries's sense, follow Mendel's law, while elementary species do not. De Vries has indicated how he supposes this difference might come about.

[1] Hybridization often brings such latent characters once more to the front.

A variety has the same number of unit-characters as has the parent species, and when the two are crossed the unit-characters pair, each with its kind, subsequently in the second generation, separating again to give the Mendelian ratio. On the other hand, when a new species arises, a new unit-character is formed that is assumed to have no pair in the parent form, hence de Vries assumes that it must divide and go to all the cells when the Mendelian characters simply separate. It is not evident why a new unit-character should be assumed to divide and an old one that has lost its pair should not divide. It seems simpler to assume that both kinds always divide, but that in the variety the condition of latency has appeared, and that this condition alternates in the hybrid's germ-cells with the old character, while in the "progressive" mutant the new character always dominates.[1]

Linnæan species are, according to de Vries, large groups composed often of many elementary species, some of which at least — if we exclude local races due to environment — take the rank of varieties of ordinary systematic writers. Linnæan species are separated from each other partly by progressive, partly by retrogressive and degressive, characters,[2] *i.e.* they may differ both by true specific differences (progressive) and also by varietal characters (retrogressive and degressive).

In this connection it is worth while to call attention to a point that de Vries has considered in regard to the *origin* of the mutation itself. The new type originates by the union of a male and a female cell — spermatozoön and egg. In which of these did the mutation first appear? If only in one, the mutation is a

[1] As stated above, de Vries ascribes the behavior in inheritance of a progressive character to the absence of a fellow-unit with which to pair. Is it not more probable that the new character is a modification of some original one which is its pair? From this point of view the behavior of a progressive character is not due to its pairing or lack of pairing, but to some inherent quality that makes it dominate in the pair. There is some evidence that all new characters do not behave in this way, and that some of them are recessive to the original characters as seen in the long hair of the guinea pigs.

[2] Progressive characters are *new* characters. Retrogressive characters are those that have disappeared, *i.e.* become latent. Degressive characters are latent characters that have become active.

hybrid. If all hybrids followed Mendel's law, which they do not in fact, we should expect a *resolution* of the parent types in the second generation. Since this does not occur in most of the mutations of œnothera, we must infer that if the mutation is a hybrid it belongs to the class of stable hybrids. This is in substance de Vries's interpretation. If, as de Vries assumes, the mutant is the result of a mutating germ-cell meeting one of the ordinary kind and producing a stable hybrid, it might appear that if the hybrid were back-crossed with the parent, the offspring should be again like the hybrid, but this was not the result found. These and other considerations show that there are some obscurities concerning the origin of the œnothera mutants. Their behavior when hybridized is also difficult to harmonize with other cases of discontinuous inheritance.

Variation and Mutation in Helix

In connection with his experiments on snails Lang has made some important observations on the relation of continuous (or fluctuating) and discontinuous variation. He has found that in certain colonies of Helix hortensis, in the neighborhood of Zurich, only two kinds of individuals exist: yellow bandless and the yellow five-banded. When inbreeding they produce only these two types again, the bandless condition dominating in the first generation as already explained. No intermediate forms appear. This is an example of strictly discontinuous inheritance.

If the banded individuals in other colonies are closely studied, it is found that the number and character of the bands vary; they are broader or narrower, they may remain separate or become united, especially the fourth and fifth bands. Their color may be dark or light. An examination of colonies from other localities shows that all transitions exist from the most highly developed five-banded condition to a bandless individual. Experiments establish that the offspring of the same parent may show these extremes. Here there seems to exist a fluctuating variability whose extremes include the two types of discontinuous

forms, or mutations mentioned above. This comparison raises the question whether the two forms of variation, fluctuating and discontinuous, are fundamentally different, or whether they are only extremes of the same process. Let us examine this question more closely.

Lang gives the following imaginary case that bears on our problem. Suppose there existed a species having three varieties, differing according to size, being 4, 6, and 8 centimeters in length. On crossing they Mendelize and do not give intermediate types. Differences in nourishment, however, may cause the size of any one of the three types to be a little larger or smaller, 2 millimeters being the extreme in either direction, but this will cause no overlapping. Suppose, however, that the fluctuations, due to differences in food, for example, are so great that the largest individual of the 4-centimeter variety is as large or larger than the smallest individual of the 6-centimeter variety. In other words, the individuals *transgress* the limits of each variety, *i.e.* the breadth of the fluctuation of the variety is so great that it overlaps the limits of the nearest related variety. Then we should have a population in which a continuous series could be traced from one extreme to the other. Apparently we should be dealing with a continuous variation, but in reality with three pure lines that overlap. Breeding experiments alone could determine that these three types actually exist. Such experiments would be comparatively simple where self-fertilization is possible; but where cross-fertilization is necessary, the separation of the population into its three true races becomes more difficult.

Lang has found in Helix hortensis somewhat similar conditions to those given in this imaginary case. It has been pointed out that while in some colonies only two sharply separated types appear, in other colonies numerous variations are found whose extremes run into each other. Within the species there exist the possibilities of eighty-nine variations in the banding, and the color may be white, yellow, orange and brown, or ash-gray. There are size varieties also, and the bands themselves may be continu-

ous or regularly broken, and these latter by fusing produce even cross-bands. A band may be absent or two bands may unite into one, etc. It is possible, as has been said, to arrange these variations so that a continuous series is formed. Lang concludes for these snails that "there exist colonies in which two forms are found that behave like well-defined *mutations*, but which are connected in other colonies by continuous series of intermediate forms that appear to be *variations*." Lang has begun an experimental examination as to whether these "variations" are themselves constant, *i.e.* whether true races exist within the population, or whether there is simply a continuous fluctuation between the extremes of the series. He has already determined that a large number of these varietal characters are inherited to a high degree. Many forms of banding exist, such as 12345, 10305, 00300, 00345, 00045, with the colors white, greenish yellow, orange-yellow, red; also the intensity of the coloring, the opacity, and the dotted condition of the bands. Even the breadth of the bands and different forms of fusion of the bands, such as 12345, 12345, 12345, are inherited. Lang states his conviction that further research will reveal that there is scarcely a single, or at least very few characters that *may* not be hereditary. In such cases it is possible to separate the pure lines from a complex population. Lang also states "that almost every character may appear at one time with the heritable character of a mutation, and at another time with the not heritable character of a fluctuating variation." The difference between a mutation and a variation must rest not on the criterion of discontinuity or of saltation on which "so much stress has been laid, but on the character of the heredity." Fluctuating variations differ quantitatively, mutations qualitatively; but Lang thinks it advisable not to draw too sharp a line between the quantitative and qualitative differences.

These studies of Lang recall the observations of Gulick on the land snails of the Sandwich Islands, where almost each valley has its peculiar variety. There seems to be in this case a highly mutable species. Experiment alone can fully settle this point.

Evolution by Means of Definite Variation

The evidence which we now possess indicates, with some probability, I think, that in some cases, at least, the process of evolution may have been by definite or discontinuous changes from one fixed form to another fixed form. The essence of the process is not that the change has been marked or great, but rather that the new type is, from its first appearance, a definite step in a new direction. What has been gained does not need to be maintained by any process of selection, but becomes a part of the permanent inheritance. It is probable that it may be found convenient to distinguish between different kinds of mutations. In fact, de Vries has already distinguished between mutations that involve only a loss of a character (leading to the formation of a "variety" — a varietal or retrogressive mutation), and mutations that are new and form new elementary species — progressive mutations; and mutations that are due to a latent character reappearing — degressive mutations. Of greater importance for the theory of evolution would be the distinction between those progressive mutations that become recessive in the first generation, when crossed with the parent forms, and subsequently split according to the Mendelian proportion, *recessive mutations;* those mutations that dominate in the first generation after a back-cross, and may or may not split subsequently, *dominant mutations;* and those that produce a new permanent form or fixed hybrid, when crossed with the parent *hybrid mutations.* Any one of these three kinds of mutations may give the starting point for a new group of organisms, a new species, or a new variety, but the chance that they may do so will be different in different cases, and this important consideration must next be examined.

It is recognized that one of the greatest difficulties that Darwin met with in his theory of natural selection was the *swamping* effects of crossing. If a new and better fluctuation were to appear, it would, in most cases, in order to perpetuate itself, have to unite with the parent form. It will be recalled that

Darwin was obliged in the *later* editions of the "Origin of Species" to assume that a beneficial variation, in order to get a foothold, must appear in a relatively large number of individuals. His critics were not slow in pointing out that if we suppose a variation to be so common that it occurred in many individuals at the same time, it is probably the result of some *definite* process taking place, and the change into a new species might be brought about in time without selection of any kind being necessary. Hence one assumption will do instead of two, and the explanation is correspondingly simplified. If we still try to save Darwin's theory by assuming that we need only suppose that half of the fluctuations in a given direction, *i.e.* those on one side of the mean, survive and furnish the basis for the next generation, and that this process repeats itself in every generation, we meet with a fact, apparently well established, that shows how futile it is to attempt to save the theory in this way. It has been shown by actual experiment that all that such a process accomplishes is to raise the average in the direction of selection, and that however long the process is continued, and however severe the selection, nothing new, no new species, can be created in this way. As soon as the selection ceases, the form quickly slips back to its original condition.

Let us see if the mutation theory can surmount this difficulty, for if mutations appear in the small numbers shown by de Vries's experiment, it may seem that they, too, might quickly become swamped by back-crossing with the parent type.

In the first place the new type is at the start different from the parent, and may be capable of living in a different locality, *i.e.* under somewhat different external conditions. Hence the chance of becoming swamped by back-crossing is lessened. If more than one individual occurs in the proper locality, the chance for propagation is given. Since the mutations in the evening primrose are produced year after year, this condition may at some time be realized. In hermaphroditic forms, moreover, the opportunity of self-fertilization exists, and this increases the chance of the mutation establishing itself.

Even if the new form is adapted to the same locality as the parent species, it may ripen its germ-cells at a different time, and this will again increase its chance of isolation from the parent species.

If the new form is only a *variety* in de Vries's sense, it will get an opportunity of surviving in another way. Suppose it does back-cross in the first generation, it will reappear in every succeeding generation, so that it may go on increasing in numbers every year. If it should be a form with better chances of survival than the parent, it may subsequently become the more common type.

It has been shown, especially in some animals, that the new mutation may dominate in crosses with the parent form. Consequently, in the next generation it may appear in many individuals, and the number of new individuals will increase in every generation. Should the new character follow Mendel's law, some of the hybrids will be pure, others mixed; but in either case the opportunity of surviving is given, and if the dominating type is at all capable of existing, it will always remain in existence, and, under certain conditions, as when, for instance, it is better suited than the parent form to another locality, it may establish itself there.

The important experimental results of Standfuss bear directly on the problem of the crossing of new mutations with the parent species. He describes a number of cases that he has himself observed, and records a number of aberrations recorded by other entomologists, in which a new type was crossed with the parent stock. A few cases are also given in which two aberrations were inbred. In both groups the offspring were either like the parent species or like the aberration, and no intermediate forms were produced. These results were obtained in the first generation of hybrids. In a few cases a new generation was also reared and the same phenomenon of splitting was observed. These results show that a new type that appears may, even if crossed with the parent species, reproduce itself in its pure form without blending. The process continuing in succeeding

generations would soon lead to the production of a large number of individuals of the new type. The possibility of the formation of a new species in this way is clearly shown. The proportion of individuals belonging to the new and to the old type varies greatly in different forms, and there appears to be a curious relation between the type produced and the sex of the individual, but with this question we are not here concerned. A single example will suffice to illustrate the character of the result. The moth Aglia tau produces an aberrant form, A. lugens. A cross between the two types produced 14 males and 28 females of A. tau, and 31 males and 13 females of A. lugens. Two individuals (F_1) of the type A. lugens belonging to the second generation (F_2) were mated.[1] They produced 3 males and 8 females of A. tau, and 49 males and 42 females of A. lugens. The results do not appear to conform to the Mendelian law, but it is not improbable that the aberration was not a pure form but a dominant-recessive. However this may be, the appearance of both types and the absence of intermediate grades is of the highest interest.

Standfuss's general conclusion is given in the following statement: A union between the parent species and an aberration that has arisen suddenly and discontinuously ("sprungweise") — a variety in the technical sense — produces in many cases not any intermediate forms, but the parental species type and that of the aberration. On the other hand, a union between the parent species and an individual of a local race showing a series of intermediate gradations produces a series of intermediate forms.[2]

If the new character is transmitted to all of its hybrid offspring and to their descendants, it will become sooner or later transferred to all of the individuals that are met with, and in time may become a part of the common inheritance.

It remains only to consider another point — one on which de Vries has recently laid some emphasis. He finds in the evening primrose that the new progressive mutations are to some

[1] Of another combination, however.

[2] This is the case apparently in the crosses described by Tutt.

extent sterile with the parent type, in the same sense that even closely related species are *often* sterile. De Vries's statement gives the impression that he regards this property of sterility as a general property of mutations. But there are other cases of mutations where nothing of the sort is evident. Such types as the ancon ram, the merino sheep, the turnspit dogs, the Japanese peacock, the guinea pig with whorled hair, certain breeds of fowls with different combs, show no evidence of infertility when crossed with the parent type. Furthermore if many of our domesticated races owe their origin to the appearance of mutations, and to the introduction of wild elementary species (which in principle may amount to the same thing), it is surprising to find no trace of sterility between the different breeds, as we should expect if sterility is one of the general peculiarities of mutations. If many Linnæan *varieties* are *elementary species*[1] that have arisen as mutations, it is well known that they are, as a rule, perfectly fertile when crossed.

It seems likely, therefore, that the sterility of some of the œnotheras may be the exception and not the rule for elementary species, and that the same principle holds here that Darwin has so ably developed, viz. that fertility is a graded process, not strictly following the lines of species and varieties, but dependent on the extent of physiological differences between two forms.

Our examination of the possibility of new mutations becoming swamped by intercrossing shows that there is no real difficulty to be met in this direction, although it is also apparent that some kinds of mutations may, of course, become lost by crossing.[2] The opportunity exists, however, for some of them, especially those that dominate, to find a place in the economy of nature. No one will pretend that all new forms that appear will survive.

[1] Some of them may be "elementary varieties," others local varieties due to external conditions, and others hybrids in which there is a blending of the new and old characters.

[2] Those, for example, in which blending occurs, for this, too, is one of the results of hybridizing even where we have reason to think that the new character arose as a discontinuous variation.

Many will be incapable of surviving, however often they appear, and even some kinds that might survive may be swallowed up again, so to speak, by the parent species.

Many further questions concerning the factors of evolution suggest themselves which cannot be answered at present. For example: if a mutation arises and survives, is another mutation in the same direction more likely than in a different direction? If a mutation is traceable directly to external factors acting on an internal condition or at a particular stage of the germ-cells, will it recur again and again in all individuals, subjected to the same conditions, or will it be confined to the descendants of those strains in which they have first "accidentally" (?) arisen? What proportion of mutations survive autonomously and what proportion by crossing with the parent stock? How many are lost by being recessive, and how often do these recessive individuals form elementary varieties? Do progressive changes take place that are definite (*i.e.* not fluctuating) in character and are too small for us to recognize them as mutations because the steps fall within the range of fluctuating variations?

These and many other questions demand to be answered by any one who attempts to apply the observed facts of mutation and discontinuous inheritance to the theory of evolution. It is obvious that until we can answer them we must remain in the dark concerning the influence on evolution, and can only suggest, but not prove, that mutations have furnished some of the materials for organic evolution.

Adaptation

The problem of evolution of organisms has become so closely associated with the question of adaptation that we must briefly refer to this question in connection with the mutation theory. If a species could be changed (so that it became a new species adapted to a new environment) by picking out those fluctuating variations of an adaptive kind, the problem of adaptation would occupy an important place in experimental zoölogy. But if this is not the case, the question of adaptation occupies a secon-

dary place, for adaptive mutations, like all others, are given; not made by selection.

If it were possible to change each character of a species, so that first in one respect, then in another, the organism would become better suited to new conditions, — molded to them, as it were, — we could imagine that the evolution of organisms has taken place in this way. The process of adapting would be the same as the process of evolving. This view assumes not only that each character may, in turn, be changed without the rest of the organism becoming seriously affected, but also that new species may be created in this way. It is this process that the Darwinian school has assumed to take place, and hence, for them, evolution and adaptation are closely similar processes.

On the other hand, the mutation theory assumes that new species appear without regard to whether the change will be an adaptive one or not. If the new form should be one suited to the old, or to some new locality, it has a chance of surviving, *i.e.* it is sufficiently adapted to exist. From this point of view the problem of evolution is a different one from that of adaptation. Moreover, it will be seen that while the process of evolution is one that can be studied by scientific methods, the adaptation of an organism is not a causal problem at all. If a new form is adapted, that is the end of the matter; if it is not, it perishes. The scientific problem deals with the origin of mutations and their causes. Their adaptation is an independent question, and depends on whether the proper external conditions exist at the time when the mutation appears. Inasmuch as only those mutations survive that can survive, we find that organisms are always adapted to the environment in which they exist, and this *condition* of living things gives the appearance of a fundamental problem where in reality no such problem exists. The causal problem is the problem of the origin of new forms; the question of their survival is only an historical question for all living species.

Under certain conditions, and in certain cases, the two problems appear, at first sight, to merge into each other. For if,

as we have supposed, external conditions may sometimes cause adaptive changes in adult organisms, *i.e.* in their body-cells, and if the egg is at times similarly affected so that the next generation shows from birth the same changes; and further if these general changes are mutations, *i.e.* fixed in character, it will appear as though the process of adaptation and of evolution has taken place at the same time. It appears, however, when the whole field of variation is examined that this is only a special case. In other cases the changes affected by external conditions may be different from those brought about in the germ-cells, and some of the new mutations may be adapted to a different environment, or to the old one in a different way. In both cases the problem is fundamentally the same, and it is the process of variation that is our real problem.

Lloyd Morgan, Osborn, and Baldwin have suggested that adult animals may at times become adapted to a new environment by a direct response, as by the use and disuse of certain organs of the body, and maintain themselves in this way until the proper germinal variations occur that fix, as it were, the new characters so that they become a part of the permanent inheritance of the species. Thus the organism, owing to its power of responsive adaptation, adjusts itself to a suitable environment and awaits the time when the fixation of the new characters may successfully be accomplished as the result of a germinal variation of the right sort. It is assumed that fluctuating variations bring about the permanent change, but obviously a mutation would give the same result. To what extent the advent of the new variation, whatever its origin, is anticipated in the way assumed, is not known. On the mutation theory it is doubtful whether this subsidiary assumption is needed to explain how new species arise. On the theory of the selection of fluctuating variations the assumption of "organic adaptation" seems to cover an admitted weakness of Darwin's theory, but whether the selection of fluctuating variations could ever fix permanently a character is a question that seems from the experimental evidence to be answered in the negative.

The Selection Theory and the Theory of the Survival of Mutations

The differences between the Darwinian *theory of natural selection* and the *theory of the survival of mutations* have been already indicated in their main features. It remains only to clear up certain minor points.

Darwin has stated his theory in such general terms that it may easily be supposed to cover also the theory of the survival of mutations. In fact, he does at times include the latter view in his theory of survival; for he believed that competition and survival take place not only between the individuals of a species (fluctuating or individual variations), but also between varieties and species themselves. The latter is, in principle, nothing more than the theory of the survival of the better-adapted elementary species. In this regard we are at one with Darwin's view. But in the application of the Darwinian theory both by Darwin himself, and especially by his followers, the whole weight of the argument has been thrown in favor of the selection of fluctuating variations. Moreover, although Darwin was perfectly familiar with the occurrence of sports, mutations, and saltations, he has argued at times that the latter cannot have given the basis for the evolution of wild species, because the laws of hybridization that govern the crosses between wild species and varieties differ from the laws of hybridization in the case of sports.

Darwin's theory dealt with the "*origin of species*," and the theory of natural selection was offered to account for the *origin* of species through the selection of fluctuation variations. Many cases are given in which it is attempted to show how individual differences become built up into varietal differences, and the latter into specific differences. In sharp contrast to this view the other theory, the theory of the survival of mutations, affirms that species do not originate in this way. Individual differences do not slowly change into specific differences. Specific differences appear suddenly as mutations. The origin of species thus becomes a very different question from that imagined on Darwin's theory of selection. *On the mutation theory selection destroys*

species; it does not originate them. The same conclusion follows if we suppose that species have been formed by the direct action of the environment, or by progressive stages resulting from internal factors (orthogenesis); the survival of the adapted new forms accounts for the general condition of adaptation of living things, but not for the origin of the adaptations, or for the origin of species. The origin of species and the adaptation of living things may, after all, be different problems. In fact, the question of what constitutes a species has given rise to widely different expressions of opinion, and the entire problem of evolution may have been prejudiced by too much emphasis having been laid on the origin of species. If we admit that species are arbitrary scholastic conventions, their origin is of secondary importance for the theory of evolution compared with the problem of adaptation of living things. It is only from the point of view of classification that the origin of specific differences is of value. If their origin is the same as that of adaptive differences between individuals, it may be that the conclusions derived from the study of specific differences may throw light on the origin of adaptive differences, but if the origin of specific differences is different from the origin of adaptive differences, the two problems should be studied separately.

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EXPERIMENTAL STUDY OF GROWTH

CHAPTER XV

EXPERIMENTAL STUDY OF GROWTH

Introductory

Normal Growth

Although growth is recognized as one of the fundamental properties of living things, comparatively little zoölogical work has been done in this field. Botanists have paid more attention to the phenomena of growth and with marked success. In almost every field of biological investigation the process of growth is directly or indirectly involved in the changes that take place; yet the connection between these changes and growth is often obscure, for as yet we know almost nothing in regard to what takes place in the protoplasm during growth, and very little in regard to the causes that incite growth or inhibit it.

In this and in the following chapters I shall attempt to give some of the most suggestive results that have been obtained regarding the growth of animals, although the purely physiological side of the question, where most, in fact, has been accomplished, will occupy a secondary place. Attention will be directed more particularly to the gross phenomena of normal growth and to the external factors that influence the growth of animals.

The process of growth may be said to begin with the egg and to end with the adult. While in some animals the adult condition coincides in a very general way with the condition of sexual maturity, in other animals growth may continue throughout the length of life of the animal, becoming smaller in amount as the size increases beyond what we may speak of as the adult condition. In a general way we may class these two kinds of growth

as *determinate* and *indeterminate*, although the distinction is of only secondary value.

Growth and differentiation are often spoken of as the two processes by which the embryo is transformed into the adult. The distinction is difficult to apply, for differentiation is often accompanied by growth and growth by differentiation.

The most general definition of organic growth is that of increase in volume. Sachs has pointed out that an increase in volume alone does not necessarily mean growth, because it may be due simply to swelling, as when a piece of dead wood imbibes water and becomes larger. He defines growth as an increase in volume accompanied by a change of form; yet a change in form is not always apparent when we have reason to think that growth has really occurred. If, however, we include in our definition of growth the idea of an *increase in the volume of the living material*, we arrive at a more satisfactory definition. Some examples of normal growth may serve to bring the phenomena before us in a more concrete form.

Davenport has measured the amount of water and of dry substance in the tadpoles of frogs at different stages of their development. His results are summarized in the following table: —

Date	Days after Hatching	Average Weight in Mg's	Weight of Dry Substance	Weight of Water	Per Cent of Water
May 2	1	1.83	.80	1.03	56
3	2	2.00	.83	1.17	59
6	5	3.43	.80	2.63	77
8	7	5.05	.54	4.51	89
10	9	10.40	.72	9.68	93
15	14	23.52	1.16	22.36	96
June 10	41	101.00	9.90	91.10	90
July 23	84	1989.90	247.90	1742.00	88

During the segmentation stages of the egg and during the early period of formation of the embryo (not included in the table) the increase in size of the embryo is not very great. After

hatching (when the records begin in the table) there is a steady and rapid growth due to the inbibition of water. The dry substance even decreases during this time. Then follows a period when the dry substance increases enormously, so that the *percentage* of water falls, but nevertheless a great amount of water continues to be absorbed, and is mainly responsible for the increase in size.

The next table gives results obtained by Potts for the growth of the chick: —

Hours of Brooding	Absolute Weight in Grams	Per Cent of Water
48	0.06	83
54	0.20	90
58	0.33	88
91	1.20	83
96	1.30	68
124	2.03	69
264	6.72	59

Here we see that the percentage of water falls in later stages, and the increase in weight must be due in a greater degree to the assimilation of the materials of the yolk. Nevertheless, there must be a continuous absorption of water from the albumen or white, for, although the percentage sinks, the amount of water is continually greater.

Similar results have been found by Fehling for the human embryo as shown in the following table: —

Age in Weeks	Absolute Weight in Grams	Per Cent of Water
6	0.975	97.5
17	36.5	91.8
22	100.	92.0
24	242.	89.9
26	569.	86.4
30	924.	83.7
35	928.	82.9
39	1640.	74.2

These results are for higher animals. In the lower animals, where the percentage of water is often very great, the results may be somewhat different, but we lack data at present on this point. The amount of water in adult medusæ is about 95 per cent; in sea anemones, 87; in sponges, 74 to 84; in the earthworm, 87; in the slug, 87; in one of the ascidians, Botryllus, 93; in the crayfish, 71 per cent. In a chick twenty-one days old, *i.e.* at the time of hatching, the water present is 80 per cent. In man there is 66 per cent of water; but this varies greatly in different parts of the body: thus, in the enamel, 2 per cent; in the bones, 22; in the muscles, 75; in the blood, 79 per cent.

The most complete account that we have at present of the growth of an animal from birth to maturity is that by Minot in his paper entitled "Senescence and Rejuvenation." I shall give, therefore, a detailed account of his results. Minot used guinea pigs for his work. The number of young born in different litters is given in the following table: —

No. in a litter	1	2	3	4	5	6	7	8
No. of litters observed	23	58	37	18	2	2	2	1

It will be seen that litters of two are most frequent, corresponding with the number of mammæ of the mother. Yet there is no close correspondence, since over half the litters contain more than two young. What the conditions are that determine the number of young in a litter is not entirely clear; one fact at least was made out, viz. *that older mothers had larger litters.* This is shown in the following table:[1] —

No. in a litter	1	2	3	4	5	6	7	8	
Average age of mothers	200.9	286	289.7	464.8	104	?	200	433	days
No. of observations	18	51	27	15	1	0	1	1	

Minot thinks that there is also an individual tendency for certain individuals to produce litters of a definite size, which is probably due to a tendency to set free from the ovary fewer or more eggs. For instance, two cases of successive litters gave:

[1] Litters of 5, 7, and 8 are based on a single observation, and Minot says have little value.

3, 1, 4, 4 young, and 5, 2, 7, 6 young. Larger litters appear on an average during warm weather. Gestation takes from 9 to 10 weeks, so that young born in July are influenced by conditions existing in May, and those in November by August conditions, etc. At birth male guinea pigs average 70.8 grams and females 70.1. The individual variation is very great. For instance: —

Largest male weighed	128 grams[1]
Smallest male weighed	35 grams
Largest female weighed	111 grams
Smallest female weighed	35 grams

The causes of this variability were in part detected. In the first place it was found that the larger the litters the smaller the pigs. "At first sight this seems easily explained as a mere ratio of food supply and demand; this would accord with certain views of Herbert Spencer, but not with the facts of nature." There must be also some other cause for the variability than the number of young, otherwise the heaviest individuals would occur only in litters of two or of one, but this is not the case. The explanation of this fact is found in the length of the *gestation* period, which is shorter the *larger the litter*. "The individuals of larger litters weigh less at birth than the members of smaller litters," *because they are born sooner* or, in other words, have not been growing so long. This is shown in the following table. The average time of gestation is 67 days.

No. of Young	Average Gestation in Days
1	68.7
2	67.6
3	66.7
4	67
5	66
6	
7	
8	

[1] An exceptional case, the next highest being 113 grams.

The weight varies also with the season of the year, probably in consequence of more favorable nutrition at certain times.

The individuals of the same litter vary in weight, as shown in the following table: —

The young differed in weight between

0– 3	grams in	12 cases
4– 7	grams in	19 cases
8–11	grams in	10 cases
12–15	grams in	6 cases
16–19	grams in	6 cases
20–23	grams in	4 cases
23–27	grams in	1 case
35	grams in	1 case

This difference in weight between members of the same litter is probably due to differences in position of the embryo in the uterus, or to the number of young in each uterus, three young being in one uterus and only one in the other. If this is true, odd numbers should show greater differences, and this is often the case.

For a few days after birth *male* guinea pigs lose weight; *females gain weight.* The females average, when born, a little less than the males, but they gain during the first days, so that they may actually then weigh more, and this "advantage is long maintained." A more minute examination shows that both sexes really lose after birth, but the *males* more; the females begin very quickly to gain, and obscure the initial loss. In both males and females the growth during the first few days is less than that from the fifth day onward. It is not until the twenty-ninth day that the male catches up, weighing 203 grams as against 203.7 for the female. When the adult condition is reached, the males weigh much less than the females. After the first month to the end of the first year the males average more. During the second year the averages are too variable for generalization, although the males weigh somewhat less on the average. During the youth of the guinea pigs one point comes out clearly, viz. that "each individual appears to be striving to reach a particular size." Thus if an individual grows for a period excessively fast, there

follows a period of slower growth; and, *vice versa*, those that fall behind make it up later, if they remain in good health. A young guinea pig may lose one third its weight from intestinal catarrh, and make the loss good later. "It is probable that the same is true of man, and that the usual and even the severer illnesses of childhood and youth do not greatly affect the ultimate size of the adult." Pagliani shows that children brought up in poverty and undersized will recover in the most surprising manner if placed under favorable circumstances.

"It has been asserted by Carpenter, Spencer, and others that the functions of nutrition and reproduction are in principle opposed to one another, because reproduction makes such a demand upon the parent for material that the supply of nutrition and growth of the parent is lessened." Unfortunately for this philosophic generalization the premises are wrong — the growing animal is not growing at its maximum of assimilative power. It has been shown that young female guinea pigs grow about the same whether they are carrying young or not. Minot concludes that "gestation does not represent a tax upon the parent but a stimulus — it does not impede growth, but on the contrary favors it." Spencer's "*dogmatic* assertions" concerning the opposition of growth and reproduction are open to justly severe criticism.

A guinea pig reaches its full size by the end of the first year, when it weighs about 775 grams. A rabbit is also full-sized a year after birth, and weighs 25000 grams. Man may be said to be full grown at the end of twenty-five years, and has then an average weight of 63000 grams. If we add to these times the length of the period of gestation, and divide the weights by these numbers, we obtain the average rate of growth a day.

Guinea pig	775 ÷ 365 + 67 days = 1.82 per diem
Rabbit	2500 ÷ 365 + 30 days = 6.30 per diem
Man	63000 ÷ 9139 + 280 days = 6.69 per diem

The calculation shows that man is larger than the rabbit because he grows for a longer period; but the daily increments are nearly

the same for both. On the other hand, rabbits attain a larger size than guinea pigs, not because they grow for a longer time, but because they grow faster. Thus there are two different ways of attaining larger size.

Senescence

After reaching a certain stage in their growth some organisms begin to "grow old." There is no very fixed period at which the decline may be said to begin, for after reaching full growth there may follow a relatively long period before any evidence of growing old can be detected. Thus in man the full growth is reached about the twenty-fifth year, but for the following ten years or more there may be little change indicating a decline. In many insects, on the other hand, the complete growth coincides very nearly with sexual maturity, and after the eggs of the female are laid the decline may follow very quickly; in fact, in some cases death follows at once, so that there is no period of senescence at all.

In some of the crustaceans, there are species in which, apparently, the individuals grow larger as long as they live, as seen in the lobster and to a less extent in crabs and crayfishes. Some mollusca also seem to continue to grow for many years, adding each year a new and larger edge to the shell. In most of these forms the period of egg laying occurs once a year. In the vertebrates we find that fishes and some species of amphibians and reptiles grow continuously, although very slowly, after a certain size has been reached — so slowly, indeed, that they may be said to have an upper limit of growth. On the other hand, birds and mammals cease to grow after a certain size has been reached that may be quickly attained.

Minot looks upon senescence as due to the loss of power to grow. He thinks that previous writers have given an incorrect interpretation of the rate of growth. They count the absolute increments of equal successive periods, but during each period the size of the body increases, and this should be considered. Under these conditions if the rate of growth were constant,

the proportionate increment would remain the same, but the absolute increments would become steadily larger. In other words, Minot believes that the rate of growth at any particular time must be measured in terms of the weight of the body at that time. He finds when measured in this way that, "first, the rate of growth diminishes almost uninterruptedly from the time onward when the animal recovers from the post-natal loss of weight; second, that diminution is rapid at first but slower afterward."

Minot shows for guinea pigs that after the post-natal retardation, the increments of growth increase from the second to the fifth day at about 5.5 per cent in terms of body weight. From this time onward the increment decreases very rapidly at first, and then more slowly. Thus from the fortieth to the fiftieth day it is 1.2; from the one hundred and ninetieth to the two hundredth day it is .2; and after 22 to 24 months about .02. Conversely, if equivalent amounts of growth are taken and compared with the time required to acquire them, we find that to increase in weight from 200 to 222 grams takes 4.9 days; to increase from 470 to 523 takes 20 days; from 697 to 766 takes 40 days. In each of these cases the weight is increased about 10 per cent. The results show a progressive loss which after a time, as in man, may come practically to a standstill. In one sense, therefore, the animal may be said to begin to grow old almost from the moment that it is born. This, however, is not what is usually meant by growing old, although the phrase has been employed in various ways. Generally we refer to the *decline* that occurs after growth has come to an end; but there may be a considerable interval in an animal's life after it has ceased to grow larger, during which time it has not begun to "grow old." On the other hand, animals that continue to grow, however slowly, as long as they live, can scarcely be said ever to grow old, although they may be very old in point of time. This brings us to the question of the length of life of different animals, and whether it can be artificially prolonged by altering the conditions of life.

Length of Life in Different Species

In contrast to the method of studying growth and senescence described in the preceding pages another method has been followed by Weismann, viz. the method of comparison of the length of life in different species.

In his essay on "The Duration of Life," Weismann has brought together some interesting data relating to the length of life of animals. He shows how meager our information is concerning the length of life of lower organisms, except in the case of those that live only through a certain season of the year, as many of the insects do. Weismann points out that it is often stated that both the duration of the period of growth and the length of life are longer for larger animals and shorter for smaller ones. An elephant may live for 200 years, a horse for 40 years, and since they both require a relatively long time to grow up, it follows that part, at least, of their life must be longer than that of a smaller animal that may reach its full age in a few months. On the other hand, other smaller vertebrates, such as certain fish — the pike and carp — may live as long as an elephant; and a cat or a toad may live as long as a horse.

Flourens thought that the length of life of an animal was equivalent to five times its period of growth. Thus if man grows for twenty years, he lives to 100; but on the other hand a horse becomes mature in four years and may live to 40 years, or ten times as long as its growth period. From this and from other cases it is evident that no such ratio as that of Flourens will hold. Neither does greater activity mean necessarily a shorter life, for some of the most active birds are the longest lived, and may live as long as do some of the sluggish amphibians.

Weismann's conclusion is that neither size, activity, complexity of structure, nor "constitution" can account for duration of life, but that it "is dependent upon adaptation to external conditions; that its length, whether longer or shorter, is governed by the needs of the species, and that it is determined by precisely the same '*mechanical process*' of regulation as that by which

the structure and functions of an organism are adapted to its environment," *i.e.* by natural selection of individual differences.

Weismann believes that "in regulating the duration of life, the advantage to the species, and not alone to the individual, is of any importance." The purpose of the individual is the perpetuation of the species, and its length of life has been regulated accordingly. As soon as the individual has performed this purpose, it "has fulfilled its duty" and may die.[1]

Weismann believes that death is essential to the species, because the individuals become injured and must be replaced by new and more perfect forms. From this, he says, follows the necessity of reproduction and the utility of death. He points out that worn-out individuals are even harmful to the species, for they consume the food that sound and reproducing individuals might make use of. Death "is not a primary necessity but . . . has been secondarily acquired as an adaptation." Plausible as this conclusion may be made to appear when stated in this abstract and general way, it will not, I believe, bear critical examination. Without attempting an elaborate refutation of Weismann's conclusion the following objections may be briefly stated:—

(1) To put the problem of senescence and death in a different category from other physiological processes, seems entirely arbitrary. Weismann's contention that death has been imposed upon each species not by internal physiological changes, but from without by natural selection, is not only paradoxical, as he states, but it seems to me a confused point of view.

(2) Is it not putting the cart in front of the horse to argue that the length of life is adjusted to the power of reproduction? It seems more reasonable to assume, if we must make some assumption, that if there is any connection between the two things, the length of life determines in a general way the cessation of reproduction; for the general decline that leads finally to a "natural death" may at its inception affect the reproductive organs.

[1] This includes the idea not only of giving birth to the new individuals, but in some cases caring for them or in protecting them during their immaturity.

(3) It seems to me entirely wrong in principle to suppose that any one function of a species can be thought of as separated from all the others and increased or decreased to any extent demanded by the theory of natural selection without altering the other functions of the organism. Even if this could be done to some extent by selection of individual differences, the change would only be temporary and disappear when the selection ceased. No one will suppose, I imagine, that in every generation the length of life of the species in relation to its power of reproduction is being regulated in this way, and, unless selection is incessant, little or nothing can be gained, because the function or structure will return to its *natural* condition if let alone. The length of life of each species is as characteristic of it as any other of its functions, and must have appeared when the species came into existence.

(4) In regard to Weismann's view as to the origin of death in consequence of the advantage conferred thereby on the species, it is only necessary to point out that if matters of this sort were decided solely on the grounds of the advantage to the species, it might often be of much greater advantage to improve the power to repair the injuries of the adult than to bring in death as a solution of the difficulty. Those animals that have reached maturity after overcoming the dangers of development and growth might be of greater use by living in maintaining the species than by dying, and if death can be determined by selection, so could no doubt the prolongation of the reproductive power (to replace accidental losses in numbers) and the power to repair.

This whole method of arguing seems to me to be so uncertain that it is unprofitable. What we need is obvious, namely, to study the physiology of the process of senescence in different groups.

If growth and length of life are simply physiological changes, why cannot the process be maintained artificially at any desired point, or why not reversed and old age grow young again? We know too little at present regarding the process of growth to make it worth while even to hazard a guess whether the growth

process could ever be maintained in equilibrium or reversed. Optimistic enthusiasts may claim that we are on the verge of this discovery, and that the day after to-morrow we may hope to begin to grow young; but we might well hesitate to take the prescription until we were certain that its action could be stopped, for it would be as awkward to disappear in an egg as to end one's life in the other direction by growing old. Nevertheless there is urgent need that the phenomena of growth be more thoroughly studied, and the work of such serious investigators as Metschinkoff shows at least that there is a wide field for future investigation in the phenomena of senescence.

Absorption of Parts by Larvæ

We ordinarily think of all parts of the body growing old at the same time, but there are some apparent exceptions to this rule. An animal that is still growing may absorb certain parts of itself, and if the absorption of the part is not strictly comparable to the growing old of the whole organism, the two processes are so similar that they invite comparison. The most familiar example is the absorption of the tail of the tadpole, although similar cases are known to every embryologist. At the time of metamorphosis the large tail of the tadpole is rapidly absorbed, and although we have many descriptions of the way in which the breaking down and absorption of the tissues occur, we have not the slightest clew as to what initiates the process. We might imagine that with the changes in the gill region and with the imperfect beginning of lung respiration the amount of oxygen absorbed is decreased, so that the blood that reaches the tail can no longer supply that part with the necessary oxgyen, hence the tissues die and are eaten up by the phagocytes. The skin of the tail might absorb enough oxygen directly from the water or air to maintain itself, in part, during this time, hence is not so seriously affected.

That the result is not due to this cause is shown by the fact that the gill respiration is maintained during the period of absorption of the tail. It might be supposed that the beginning of lung respiration that takes place at this time might be connected

with the result. Some experiments that I have carried out disprove this suggestion also. The lungs of tadpoles about to transform were removed at the base. The animals underwent their normal metamorphosis, as when the lungs are present. Not only was the tail absorbed, but the gills also. If the operculum that covers the gills is removed so that the gills are exposed to the water, they become absorbed at the proper time. How far these changes are comparable with senescence remains to be shown.

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CHAPTER XVI

EXTERNAL FACTORS THAT INFLUENCE GROWTH

In the last chapter we studied some of the characteristics of normal growth. In this and in the following chapter the external and internal conditions that modify growth will be considered.

In anticipation of what is to follow I may state that while the *rate* of growth may easily be accelerated or retarded, the *character* of the growth is more difficult to modify. The following external agents have been found to affect the rate, and in some cases the character of growth: (1) Food; (2) Stimuli; (3) Salts; (4) Heat; (5) Light; (6) Gravity; (7) Electricity; (8) Pressure and Contact.

Influence of Food

To a certain extent the rate of growth depends on the amount of food. It is clear that if less food is obtained than needed to make new tissues, the rate of growth must slacken. On the other hand, if more food is given than can be assimilated, the rate of growth is not thereby increased. This is, however, by no means the whole question; for animals show a curious regulative power, and store up reserve materials usually in the form of fats when an excess of food is taken which may be drawn upon later if the food supply temporarily diminishes. Let us take an imaginary case. Suppose an individual to be growing at its normal rate with an abundance of food. If a certain small amount of this food is taken away, it does not follow that the rate of growth will correspondingly decrease. Take more away and the rate will decrease somewhat, but again not in proportion to the amount removed. The same fact is brought out in another

way in Minot's experiments with pregnant guinea pigs not fully grown. Not only did the mother grow at the normal rate, but she supplied the embryo also with a large amount of nourishment.

We can account for the facts on the assumption that when less than the optimum is given more substance is digested from the food, and when more than the optimum is taken proportionately less is absorbed or assimilated. The appetite of the animal furnishes in a measure an index of the amount needed for growth and repair, but one that cannot be entirely relied upon.

The size of the adult stage of some of the lower animals is much affected by the amount of food that can be obtained. There is, however, an upper limit that is quickly reached when food is abundant that cannot be surpassed. Most of the variation in size lies below this condition. For example, fresh-water planarians if kept without food for several months decrease in size, and finally may be not more than about 1/15 of the original volume. If such a starving worm is cut in two, each piece still has the power to regenerate the missing part, drawing on or making use of the starving tissues in order to make the new growth. Thus, although the worm is starving it will grow relatively rapidly at the cut surface and produce a new part. If a starving earthworm is cut in two in the middle, the anterior piece makes a new tail, and the posterior piece also regenerates a tail (reversed in direction) at the anterior end of the piece. In the latter case the old part continues to waste away, while the new reversed tail continues to add new segments to its growing end. Thus while starvation is taking place in the old piece, growth goes on in the new, and the latter must derive all of its material from the starving portion. In the "winter" salmon of the Rhine the tissues of the body are used as food after the fish have entered fresh water, when they cease to feed. These salmon may live for months (from 8 to 15, according to Meischer) without food. At the end of this time the fish are much emaciated. During the period of starvation the eggs develop. There can be little doubt that a starving mammal, if pregnant, would

continue to supply nourishment to the young in the uterus; and while the embryos might not grow as fast as do those in a well-nourished individual, they would probably grow at least as long as reserve material was present in the mother, and perhaps even while the formed tissues of the mother were slowly being used up. It would be interesting to carry out a series of exact experiments of this kind on such animals as rats, mice, or dogs — especially on forms that can go a long time without food.

These conditions show plainly that growth depends on other factors as well as on the amount of food that an animal obtains, or has in reserve.

Not only the amount of food but the kind of food also has an important bearing on the rate of growth. Yung fed tadpoles on several kinds of food, including aquatic plants, the jelly of frogs' eggs, yolk of hens' eggs, white of hens' eggs, fish, and beef. The results are shown in the following table: —

Kind of Food	Aquatic Plants	Jelly of Frogs' Eggs	Yellow of Hens' Eggs	White of Hens' Eggs	Fish	Beef
Length of tadpole	18.3	23.2	26.0	33.0	38.0	43.5
Breadth of tadpole	4.2	5.0	5.8	6.6	8.8	9.2

Fed on beef the tadpoles grew nearly three times as fast as on plant food. The experiments were continued, in some cases, to the time of metamorphosis. The large tadpoles transformed first, but the smaller ones not until they had grown large. Cuénot has also reared tadpoles under different conditions, and has recorded the time of their metamorphosis. He also found that the well-fed animals transformed first. Barfurth has shown, on the other hand, that starvation *just prior* to the time of metamorphosis hastens the change.

Experiments made by Lawes and Gilbert have shown that "growth tends to increase with the quantity of nitrogeneous food." A curious instance confirmatory of this conclusion is given by Prösher. He compared the times required by different mammals to double their birth rate with the composition of the milk of the mother. His results are given in the following table.

Man is taken as the standard, and the time required by the other forms to double their birth rate is given in fractions of that of man.

	Relative Time to double Wgt.	Fat	Sugar	Albumen	CaO	P_2O_5
Man	1	3.5	6.6	1.9	1	1
Horse	$\frac{1}{3}$	1.1	6.1	2.3	4	3
Ox	$\frac{1}{4}$	4.5	4.5	4.0	5	4
Pig	$\frac{1}{10}$	6.9	2.0	6.9	–	–
Sheep	$\frac{1}{18}$	10.4	4.2	7.0	8	9
Dog	$\frac{1}{22}$	10.6	3.1	8.3	14	10
Cat	$\frac{1}{33}$	3.3	4.9	9.5	–	–

It will be seen that the rate of growth is proportional to the amount of albumen in the milk. Thus the kitten doubles its weight in 1/33 of the time required by the human infant, and the milk contains five times as much albumen. It is improbable that the results are due solely to this factor, but that an internal factor largely regulates the growth of the young. Were this not the case, we should find that a baby fed on sheep's milk would doubt its weight eighteen times as fast as a baby fed on human milk.

Stimulants affecting Growth

I have already stated that the rate of growth is not simply a question of the amount or of the kind of food. In fact, growth depends in some cases on a *response to a stimulus*, and the amount of food stuffs converted into tissues sometimes depends on the presence of a stimulus. For example, the embryo in the uterus of the mammal appears to supply such a stimulus. Many chemical substances "that are not themselves food may stimulate the growth processes." Just as certain poisons accelerate the movements of animals, so may they also accelerate metabolic processes and lead to increased growth. "Schultz found that various poisons, such as corrosive sublimate, iodine, bromine, arsenious acid, increase the activities of yeast in fermentation."[1]

[1] Davenport, "Experimental Morphology."

It has also been shown for other molds, Aspergillus, Penicillium, and Botrytis, that alkaloids and other poisonous substances if present in small amounts accelerate growth.

Few cases of this sort can be given for animals. The best-known case perhaps is that of lecithin. Danilewsky has found that lecithin has a marked influence on the rate of growth. Tadpoles were placed in a solution containing one part of lecithin to 15000 parts of water. The rate of growth of the tadpoles was compared with that of similar tadpoles kept in water alone. The results are given in the next table: —

	Water	Lecithin
June 12	11 mm.	18 mm.
June 21	12 mm.	18 mm.
July 18	13 mm.	21 mm.
Aug. 5	15 mm.	27 mm.

The lecithin tadpoles are three times heavier and nearly twice as long as those in water alone. The results are ascribed to the stimulating effects of the lecithin. I do not feel convinced that this is the case, because any one who has reared tadpoles in confinement must have found that great variations in size are found in different dishes in which the conditions seemed to be the same. Even in the same dish very great differences in size are also found.

Danilewsky claims to have obtained similar results with young rabbits and dogs by injecting solutions of lecithin into them at intervals. Desgrey and Zaky have also studied the influence of lecithin on growth, and reach the conclusion that the beneficial effect is due to the stimulating effect of the substance. Hatai also has found that in young rats lecithin causes an increase in weight whether given as injections or with the food.

Effects of Salt on Growth

The eggs of many animals, especially those laid on the land, contain a sufficient quantity of materials to carry them through

their early development until the embryo hatches and begins to feed for itself. It appears, however, in the case of some water animals that the egg or the early embryo derives some of the materials necessary for development from the surrounding medium. In the development of the eggs of the lower marine animals it has been shown that certain inorganic constituents of the sea water enter directly into the embryo and take part in its growth. The most thorough study of this sort that has been carried out is that of Herbst. His final conclusion is that for normal growth all of the common constituents of sea water are necessary. For a few of them other closely related chemical compounds may be substituted, but it is surprising how little substitution of this sort is possible without altering the normal processes of growth. In such cases it must not be overlooked that the egg itself is a storehouse of food materials, and that the growth consists mainly in adding water to the materials already present; but there can be no doubt that extraneous salts are also fixed by the tissues of these organisms and take a part in the growth. For example, the young embryo of the sea urchin produces a calcareous skeleton. Unless calcareous salts are in the water, the skeleton is not formed; even other closely related salts cannot be substituted. Quite recently Maas has carried out an experiment with sponges. He finds in them also that unless the calcareous constituents of the sea water are present, no spicules are formed, and the development does not extend beyond a certain point.

By adding salt to fresh water the density may be increased. By diluting sea water its density may be decreased. Both changes may affect the rate of growth, as shown by the following experiments. Yung (1885) added 2.0, 4.0, 6.0, 8.0 grams of sea salt to 1000 grams of fresh water, and placed frog embryos in the solutions. In the .2 per cent solution the rate was nearly the same as in pure water. Retarded development occurred in all the others. In the .8 per cent solutions the tadpoles hatched 17 days after the normal time.

It is not altogether clear in this case whether the effects are

due to a difference in density or to an injurious effect of the salt. Control experiments should have been made with different solutions of such substances as sugar or urea.[1]

Frazeur tried the effects of solutions of sodium chloride on the rate of regeneration of Nais. The twelve anterior segments were first cut off and placed in solutions of different strengths. After ten days the number of new segments that regenerated was counted. The results are shown in the table: —

Solution	No. of Individuals	Average No. of Segments Regent per Day
Water	15	2.13
0.125 NaCl	5	1.72
0.188 "	16	1.42
0.250 "	7	1.19
0.375 "	5	1.18
0.500 "	5	1.14

Sargent has studied the rate at which the process of fission takes place in Dero vago. Ordinarily Dero doubles its numbers every ten days. The worms were kept in solutions of sodium chloride, magnesium sulphate, calcium chloride, magnesium chloride, and potassium chloride. The results seem to show that the rate of multiplication falls off rapidly with an increase in the strengths of the solutions employed.[2] As the results stand, it is not clear that they are due, solely, to the increased osmotic pressure, but the salts themselves or their ions may have been directly injurious.

Loeb has shown that the new head of the marine hydroid Tubularia grows longer in diluted sea-water than in pure sea water, and he thinks the results must be due to a change in the osmotic pressure of the solution. This might be tested by first diluting the sea water and then bringing up its osmotic pressure

[1] In some recent experiment that I have carried out I found that the eggs of the frog are affected both by the osmotic pressure and by the chemical substances.

[2] These results of Frazeur and of Sargent are taken from Davenport's "Experimental Morphology."

by a sugar solution to that of normal sea water. If the increase in length still occurs, the results must be ascribed to the chemical effects of the salts rather than to the osmotic pressure.

Effects of Heat on Growth

Of the external factors that influence the rapidity of growth, temperature has long been known to have the most influence; and since heat facilitates chemical reactions, it is generally assumed that it acts in the same way in the organism.

Higgenbotham kept frogs' eggs at 60°, 56°, 53°, 51° F., and found that they hatched respectively in 9, 14, 20, and 20 days, and changed into frogs in 73, 161, 171, and 235 days.

The rate for tadpoles has been measured by Lillie and Knowlton (1898) and by O. Hertwig (1898). For the tadpoles of *Rana virescens*, and of the toad, *Bufo lentiginosus*, Lillie and Knowlton obtained the following results: —

Temperature	Frog	Toad
9–10.9	4.5	3.0
11–12.9	5.3	5.3
13–14.9	4.3	15.5
15–16.9		16.3
17–18.9	9.5	
19–20.9	19.8	21.2
21–22.9		
23–24.8		41.3
25–26.9	31.5	39.0
27–28.9	40.0	
29–30.9	47	36.8
31–32.9	40.2	55.3
33–34.9	43.5	

The rate of growth for the frog increases up to nearly 30° C. and then decreases. The upper limit for the toad is about the same or a little higher.

Hertwig has compared the rate of growth of tadpoles of *Rana fusca* at different temperatures. Their maximum nor-

mal growth takes place at 25° C. At this temperature tadpoles develop as far in 24 hours as do those at 16° in two days. I have found that the young tadpoles of *Rana palustris* kept at a temperature of 2 to 2.5 C. develop scarcely at all, and may be kept for at least a month in practically the same condition.

Rauber states that the eggs of minnows and salmon, which develop during the winter season, will not grow above 12–15°, but do grow at 0°. On the other hand, it is known that those fish that deposit their eggs in summer develop faster at temperatures higher than these.

The optimum temperature for development of the hen's egg is about 38° C., but it will slowly develop at 25° C. The maximum point at which development takes place normally is 42°. The following table shows the rate for the chick: —

Temperature . .	34°	35°	36°	37°	38°	39°	40°	41°
Index of development	0.65	0.80	0.72	?	(1.00)	1.06	1.25	1.51

Most other animals have a much greater range at which normal development occurs. It is evident that for each species of animal there is an optimum temperature for growth, which is very different in different species. Somewhat above the optimum temperature, growth may be more rapid although less normal; but as higher temperatures are reached, the development is interfered with very greatly. A much wider range of possibilities exists for lower temperatures. This difference is probably due to the coagulation of the protoplasm. Slightly above the optimum temperature the colloidal substances of the protoplasm become coagulated. It requires much greater change in the other direction, *i.e.* for lower temperatures to coagulate the colloids. In many cases a freezing temperature is necessary to produce this effect, but even this temperature is not injurious to many animals.

Effects of Light on Growth

In studying the effects of light on growth one must be careful to exclude the heat rays. This can be done by interposing a screen containing solutions that absorb the heat rays and allow

the light rays to pass through. Furthermore by light we usually mean sunlight or "white light," which is a composite light made up of vibrations of different lengths that we recognize as colors. One of the most unexpected facts in regard to the influence of light is that in plants light is antagonistic to growth, although light is necessary for the normal existence of all green plants. The paradox finds its explanation in that most of the actual growth takes place at night; while light is a form of energy necessary to fix the carbon of carbon dioxide in the chlorophyll body. Out of this carbon and other things the starch is formed, and starch when transformed into sugar is the food of the plant supplying the material for growth. Davenport has pointed out "that it is noteworthy that embryonic tissue, and indeed the entire embryonic individual, is usually sheltered from sunlight. In animals the embryo is sheltered in the darkness of the maternal body; in birds and reptiles the egg shells are more or less opaque, and, moreover, the whole egg is usually hidden from light." Blanc (1892) has shown that the development of the hen's egg is much retarded if subjected to light.

Many animals hide their eggs, but whether this has only the advantage of concealment from enemies, or of placing them out of the light, we do not know. On the other hand, pelagic fish eggs are exposed during the day to the full light, and yet develop normally. Maupas found that ciliate infusoria multiply equally fast in the light and in the dark. Experiments have also been made with tadpoles. Edwards in 1821 stated that tadpoles would not develop at all in the dark. Later Higgenbotham (1850 and 1863) and Macdonnell showed that they grow at the same rate in light and in the dark. Yung also made a study of this problem. His results are given in the following table. In each case "typical" tadpoles were measured in each lot.

	Light	Dark	Relation Size
Lot 1, 30 days' length	23.1	19.6	117
Lot 1, 60 days' length	32.1	30.3	106

The table appears to show that tadpoles grow faster in light, but it may be doubted whether this is due to the influence of the light on the tadpole itself rather than indirectly to the influence of light on the plants that grow in the water, which are used by the tadpole as a part of its food. Possibly also the setting free of oxygen by these plants during the daytime may make the conditions more favorable for growth. Too much caution cannot be used in considering all possible sides of the experiment.

Yung also made experiments with other animals. Two hundred fertilized eggs of the trout were put into four liter vessels, and kept in running water. Those exposed to daylight hatched a day sooner than those in the dark. In this case the question of food does not enter into the problem, and the running water would seem to equalize other conditions. The eggs of the pond snail, Lymnæa, hatched in the light in 27 days; in the dark in 33 days.

It has been known for some time that for plants the blue rays act more nearly like white light, while the yellow rays give more nearly the effect of darkness. Some work has been done with animals to test the effects of light of different colors. Yung finds that *Hydra viridis* dies if kept in the dark. It grows more rapidly in violet light than in green, and in green than in white, and in white than in red light. Since hydra contains green bodies supposed to be green algæ, the influence of light is probably on the algæ, and it is significant to find that the order of colors given is, in a general way, found to have the same effect on green plants; but it is doubtful whether these results can be accepted as final, because it is not evident that sufficient precautions were taken to have the intensity of the light the same in all cases and the food conditions also identical.

Yung also carried out some experiments with tadpoles reared behind screens of nearly monochromatic colors (solutions). At the end of a month three tadpoles taken at random gave the following results: —

	Average Length	Length compared with White Light
White	24.4	100
Violet	28.5	117
Blue	25.6	105
Yellow	24.3	99
Red	20.3	83
Green	16.9	70

Here also I question whether the results have any certain value because of the variability shown by tadpoles reared in dishes, and on account of the difficulty of keeping the other conditions the same.

Vernon's results with sea-urchin larvæ are more significant, because the growth, in this case, depends little, if at all, on the food supply.

	Length
Semi-darkness	+ 2.5
Complete darkness	− 1.3
Blue (copper sulphate)	− 4.5
Green	− 4.8
Blue (Lyons blue)	− 7.4
Red	− 6.9
Yellow	− 8.9

In violet light all the larvæ died, owing to bacteria. The order of growth for the other colors was: white, blue (copper sulphate), green, red, blue (Lyons blue), yellow. The order is so different from that given by Yung that, although done on different animals, the interpretation of the real influence of the light is probably open to question.

Beclard found that the eggs of the fly, Musca carnivora, when reared under different colors developed fastest in violet light and most slowly in green. The sequence for all the colors used is violet, blue, red, yellow, green. This order agrees more

nearly with that given by Yung for tadpoles than with that of Vernon for the sea-urchin larvæ. It is noticeable that in all cases the violet stands near the top of the list, but the order of red, green, and yellow is not the same in any two cases.[1]

Growth toward the Light; Phototropism

The turning of plants toward the light is a familiar phenomenon. It is brought about by more rapid growth on the shaded side.

Most animals are free to move, and some of them move toward or away from the light. Such turning cannot be called a process of growth, but is due to contraction of the muscles of the body. Sense organs, muscles, and nerves are the physiological agents in the process. But some animals that are fixed turn toward the light, and in these the process seems more nearly to approach the condition in plants, although it remains still to be determined whether, in reality, the method of turning is the same in the two cases. One of the serpulid worms, Spirographis, lives in a tough tube formed as a secretion of its body. If illuminated from one side the worm turns toward the light, causing the tube to bend in this direction. As additions are made to the tube, the new part is made in the direction of the source of light. Here there cannot be said to be a growth of the animal, but only a growth of the tube.

The stolons of the hydroid, Sertularella polyzonias, grow away from the light, while the hydranths grow toward the light. In another hydroid, Eudendrium, the hydranths also grow toward the light.

In these cases the bending appears to be more nearly like that of plants, but, as I have said, the way in which the bending occurs has not yet been sufficiently examined.

[1] Yung found the development of Sepia officinalis to be affected by light in the following order: violet, blue, yellow and red, green. Fatigat (*Compt. Rendus*, LXXXXIX, December 1879) found for infusoria that violet light accelerated and green light retarded the development.

Influence of Gravity on Growth

It is well known that gravity has an important influence in determining the direction of growth in plants: roots turn and grow downward, stems upward. In most animals, on the contrary, gravity appears to have no determining influence on growth, although an important influence in the orientation of some freely moving forms. In animals that are fixed we might expect to meet with a response to gravity similar to that in plants, and this has been found to occur in a few cases. It is a matter of general observation that most fixed forms grow at right angles to the surface to which they are attached, but in many cases the direction of their growth cannot be due to gravity, for the surface of attachment may be oblique or even vertical. In such cases contact reaction, *i.e.* stereotropism, or some tropism other than geotropism, must determine the direction of growth. In several species of hydroids, however, it has been shown that gravity determines the direction of growth. Loeb has shown that stolons of Aglaophenia, if they do not come in contact with a solid body, grow out at first horizontally and then downward. Another hydroid, Antennularia antennina, also responds to gravity. Pieces of this hydroid produce new stems that grow upward, and stolons that turn downward. This is strikingly seen when a piece is put into an oblique position. New stems arise from the upper parts of the old one and stolons from beneath. Even an inverted piece was found to produce a root from its lower or distal end, and a stem from its upper or basal end. Stevens has shown for A. ramosum that the level at which the piece is cut off is a more potent factor in the result than gravity. Driesch observed in a species of Sertularia that whenever he altered the position of the piece the new growth changed its position so that the new part turned away from the center of the earth.

These are the only cases in which a response to gravity has been recorded. How the response is affected is not known, but it is not improbable that the result may be caused by the rearrangement

of the content of the cells, so that the heavier parts sink downward and the lighter rise upward. This interpretation finds its chief support in the fact that in plants when a centrifugal force is substituted for gravity the direction of growth is thereby determined; and also in the fact that in the frog's egg an actual rotation of the protoplasm has been observed.

Effects of Electricity on Growth

There is even less to be said on this subject than in the case of gravity. Certain writers have found that a current of electricity running at right angles to the axis of an embryo chick either brings the development to an end or causes abnormal development.

Roux placed the unsegmented eggs of the frog between two electrodes and found that the pigment arranged itself around two centers corresponding to the magnetic poles. After segmentation, each cell showed a similar arrangement of its pigment. No influence was found on the direction of the cleavage planes, and normal development took place. The cause of the arrangement of the pigment granules is not clear, nor is it understood why, in each cell, a separate center was formed. Whether the current actually passed through the egg or only over its surface is not certain.[1]

Pressure and Contact

That the growth of parts of an animal may be changed by pressure is a familiar experience. Our own epidermis responds to pressure, and even such resisting structures as bones respond most surprisingly to continued pressure, as when, for example, a new socket can be made in the pelvis for the head of the femur, or when the shape of the head of the children of savage races is altered by pressure, or when the ribs of women become deformed as a result of lacing.

A direct response to contact is best shown in fixed animals.

[1] Rossi repeated this experiment and found abnormal cleavage and abnormal development.

Thus the stolons of "hydroids and of bryozoans of some of the compound Ascidians" cling to a substratum with which they have come into contact and refuse to leave it, following all of its irregularities. Even the under surface of the film on the top of water will call forth this response.

In the development and regeneration of new parts from a piece of the stem of Tubularia a response to contact can easily be demonstrated. If a new hydranth of Tubularia on emerging from the stem comes into contact with a solid body, it turns away from it and grows at right angles to the surface of contact. If, again, the basal end of a piece of the stem of Tubularia comes in contact with a solid, it develops a stolon (and not a hydranth). On the other hand, the oral end if brought into contact with a solid develops a hydranth, *i.e.* it does not respond to contact. Other hydroids, however, will develop a stolon at the oral end if this touches a hard surface.[1] I have suggested that the contact reaction between the cells in different parts of the body may be one of the important factors in determining not only the molding of the form of each organ during the development, but that the pressure relations of the parts may be an important factor in their growth.

The Formation of Galls

The formation of galls is a remarkable phenomenon of growth, for galls are well-defined structures, differing from anything else that the plant normally produces. The best-known galls are those found on the higher plants and are caused mainly by insects. A few gall-like growths also occur on animals, as in the case where certain crustacea infesting corals cause gall-like swellings to appear. Perhaps the cyst on fish caused by the parasitic larvæ of the fresh-water mussel, Anodonta, may also be considered a gall, as well as the cysts found about parasitic trichinæ, chigoes, etc.

The galls that have been most studied are those on plants,

[1] See Loeb (1892).

particularly those on the oak, willow, and rose. The most common of these contain the larvæ of gallflies. Adler and Beyerinck have studied experimentally the process of gall formation by gallflies, and their results have thrown much light on the processes involved. Previously it had been generally held that the growth leading to the formation of the gall is caused by a poison injected by the insect at the time of deposition of the egg. The swelling caused in animals by the sting of bees, for instance, may have led to this idea; but it has been shown that, in most cases examined, the secretion poured over the egg at the time of deposition only serves to fix the egg in place. It has also been shown that the poison of the bee does not produce a swelling or a gall when injected into the young tissue of a plant. Most galls do not begin to develop until the larva hatches and fastens its jaws in the surrounding cells. In only two forms has it been shown that a secretion may be responsible for the gall formation, which begins at once and is far along before the egg hatches. It has also been supposed that the wounding of the tissue caused by the puncture of the ovipositor is responsible for the growth, but this has been entirely disproven, because some forms, the Cecidomyidæ, do not pierce the tissue, but push the ovipositor into the bud without wounding it; also because the wounded part does not, as a rule, produce the gall, but only the region around the larva; the egg itself may be placed on a free surface not pierced by the sting. Furthermore, in some cases, the plant is pierced a long time before the gall develops, the latter occurring only when the larva emerges; thus Trigonaspes crustalis pierces the young leaf in May, but the larva does not hatch until September, and then the galls begin to develop.

The galls become the abode of other species of gallflies and of other insects, parasites, and inquilines. When the larva that makes the gall is parasitized by the invading insects, the growth of the gall stops, as a rule, when the larva that made it is killed; but there are a few instances known in which the presence of the parasite seems to suffice to cause the continued growth of the gall, although it does not appear that the parasite

can itself start the gall. Inquilines, or guests, also frequently occur in galls. They appear to have, in most cases, no effects on the gall-growth so long as they do not injure the gall maker.

Most of the species of gallflies show an alternation of sexual and parthenogenetic generations, both generations producing galls, generally on the same species of plant, but the gall may differ somewhat in character. Adler has studied especially the galls of the oak. He collected the galls and kept them under proper conditions until the gallflies emerged. He placed these on the leaves of young twigs of little oak trees grown in pots, covering the branches with gauze to confine the flies. The buds that were pierced were marked with threads and their history followed. The life history of one of the species of gallflies will serve to illustrate the details of gall formation. Neuroterus lenticularis produces galls on the under surface of oak leaves, sometimes forty to fifty on one leaf. The galls are 4 to 6 millimeters in diameter and of a yellowish red color. They appear in June, and, maturing in September, fall from the leaves to the ground about the beginning of October. At this time the larva is still minute and requires much moisture for its subsequent development. If the galls are laid on damp soil, the larva will develop, at house temperature, in about four weeks; but out of doors, under natural conditions, the flies do not emerge until April. Adler put the galls in pots filled with earth which were then sunk in the soil. Each pot was covered with gauze to confine the gallflies when they emerged. He placed the flies on his saplings and saw them pierce the buds. The ovipositor is pushed under one of the bud scales as far as the base of the bud, which is then penetrated from without inward, and the egg is then deposited in the bud. When the young leaves develop the gall is very small and difficult to detect, but soon grows rapidly. Relatively few of the buds pierced produce galls, because apparently of the difficulty in placing the egg in exactly the right place. The fly that emerges from the gall in June is known as Spathegaster baccarum, and until its connection with Neuroterus lenticularis

was shown by Adler's experiments it had been supposed to belong to a different genus. The gallflies of Spathegaster are both males and females. The males emerge first, and as soon as the female appears copulation ensues. If the fertilized females are placed on oak saplings having tender young leaves in actual growth, these are pricked on the under surface. Galls begin to develop after two weeks, and remain on the tree until the autumn. The fly that emerges from these is Neuroterus lenticularis, which completes the cycle.

Other species of gallflies have only one generation a year, which is parthenogenetic. Others still may have two parthenogenetic generations a year, and consequently no sexual reproduction at all. There is great diversity in the kinds of galls. In fact, the galls often differ more from each other than do the species of gallflies that produce them, and are more easily identified.

Three points in the formation of the galls are especially interesting. First, the gall develops always from unformed tissue, particularly from the meristem of the plant. Second, the kind of cells and tissues that form the galls are those peculiar to the plant on which the gall develops; but while some of the cells may retain to a large extent their original structure, others become changed. Spiral vessels grow into the gall and ramify through its walls in definite courses. Third, while the growth begins in the vicinity of the larva, the principal changes may not be in this part, but removed some distance from the larva, especially in the more complicated forms of galls. There can be little doubt that something set free from the larva affects the cells and causes their remarkable growth. Furthermore, the stimulus must be kept up if the gall is to continue to grow. We can easily imagine that very small quantities of the stimulating substance, continually applied, are effective in producing the change, and we can see, if this is the case, how difficult it may be to imitate artificially such a process; yet experiments along these lines should be undertaken, for, if gall-like growths could be artificially induced, we would have a better means for studying the processes involved.

Beyerinck made a careful study of the galls of the willow (Salix amygdalina) produced by the gallfly, Nematus capreæ. This case is especially interesting, since the galls begin almost at once to develop, and may be full sized before the larva hatches. The cause of the growth in this case is the albuminous secretion that the gallfly injects along with the egg into the leaf. That the secretion and not the egg is the cause of growth has been shown by puncturing, and thus killing the egg with a fine needle. The gall continued to develop. This gallfly deposits its egg in the young leaves of the willow in the early spring. The gall can be detected within two days and has finished its growth in three weeks. The larva feeds on the inner wall of the gall, and finally bites a hole in one side through which it escapes after the gall falls to the ground. It then spins a cocoon and in August the adult fly, the second generation, emerges. It seeks young growing buds of the willow and pierces them. The gall develops in the autumn and falls to the ground with the leaves. The larva spins its cocoon, inside or outside the gall, and overwinters in this condition. In the first generation, in the spring, there are no males; in the second generation occasionally males may be found, but nevertheless Beyerinck thinks that this generation also reproduces by parthenogenesis.

Beyerinck has discussed the question of the kind of changes that occur when a gall is produced, and he has carried out some experiments that bear on this important question. He tried to determine whether the cells of the gall are permanently changed, *i.e.* whether their structure has been so affected that whatever they produce will be different from the tissues of the parent plant from which they arise; or whether the change is only temporary, depending on the presence of some substance exciting them to a peculiar mode of growth. The latter view seems to him the more probable as shown by the following facts: If the leaves are removed from a twig bearing the so-called "willow-rose" gall, new buds grow out of the axils of the leaves of which the gall is made. The first leaves are somewhat modified, like those of the "willow-rose," but the later leaves are like

the leaves of the normal plant. The same result was obtained with the witches broom (Hexenbesen) of the birch (caused by Phytoptus betuli). Similarly for the Bedegar of the rose caused by Rhoditis rosæ. Again, the galls produced on the grass, Poa nemorales, by Cecidomyia poæ, send out rootlike processes, and if these are covered with earth, they produce true roots that resemble histologically those of the grass in every respect. Thus the gall itself stimulates a part of the plant to produce roots that never does so normally, and these roots are similar to the normal roots of the same plant, although arising from the gall. The galls of Nematus viminalis produced on Salix purpurea fall to the ground in the autumn and may remain alive through the winter. In the spring they may increase in size, develop more chlorophyll, and produce lenticels over the surface. Beyerinck succeeded, by keeping these galls on moist sand, in causing them to produce roots from the inner surface, and these may even protrude through the opening in the gall. The roots are like the normal roots of the plant that produced the gall.

The nature of the substance injected along with the egg into the leaf by Nematus capreæ is unknown, except in so far that it is an albuminous matter secreted by glands connected with the ovipositor. Its amount is exceedingly small, both the egg and the surrounding secretion measuring not more than 0.06 millimeter, and more than half of this mass is taken up by the egg. The gall produced is about 10 millimeters in diameter. The disproportion in size is so great that Beyerinck suggests that the substance injected contains an enzyme that acts on the cells of the plant and excites them to the growth that leads to the formation of the gall.

Some species of Aphids and of Phylloxerans also produce galls, many of them of remarkable size and beauty. The stem-mother after emerging from a winter egg crawls out on to the young leaves and affixes herself at one spot on the under surface, and begins to suck the juice of the plant. Her presence, or more probably some secretion that flows from her proboscis into the wound, excites growth on one or on both sides of the leaf. A hollow gall

begins to develop, in the middle of which sits the stem-mother. She soon begins to give birth, parthenogenetically, to offspring which also remain in the gall, and in some cases hundreds of individuals almost filling the interior are produced in one or more generations. These also suck the juices of the plant by thrusting their proboscides into the inner walls of the gall. The gall may continue to grow during the whole summer, but generally its full size is soon attained. The winged insects emerge from a preëxisting opening in the gall, or in some cases the gall bursts when the inmates are mature. The phylloxerans produce galls on the leaves of hickories and other trees, and on the roots of the grape vine. Large bottle-shaped galls are produced by aphides on the elm; the coxcomb galls of the elm also owe their origin to them. The cause of the development of the galls in these cases is entirely unknown. Possibly the stem-mother and her offspring that suck the juices of the plant by thrusting their beaks into the inner walls of the gall may secrete some fluid that acts on the tissues of the plant.

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CHAPTER XVII

GROWTH AND REGENERATION

When an animal reaches a size that is characteristic for the species it ceases to grow, and it may appear that this happens because the cells of the body have lost the power of further growth. That the cessation of growth is not due to such a loss of power is shown by the ability of many animals to regenerate a lost part.

In some animals practically all the organs of the body show this remarkable regenerative power, so that there can be no doubt that the cessation of growth is not due to the loss of power of the cells to grow, but rather to something that inhibits their growth.

One of the most curious facts connected with the regeneration of a part is its rate of growth at different levels. If the tail of a fish or of a salamander is cut off near its base, the new part grows faster than when the tail is cut off nearer to the tip. Moreover, the new part that arises from the basal cut grows more rapidly at first and more slowly later. What is the meaning of this difference in rate? The result cannot be explained as due to differences in the food supply at different levels, for the rate of growth is very little affected whether the animal is fed or starved. The difference in rate cannot be explained as due to a difference in the material at the two levels, because the material derived from the base, that grows more rapidly for a time, begins also to grow less rapidly as the new part gets longer, and behaves in this respect in the same way as the material derived from nearer the tip. The difference does not seem to be due to the difference in size of the two surfaces, except perhaps at the very beginning, for in other forms, in the earthworm, for example, the same

difference of rate is found even in a greater degree, and the two surfaces are practically of the same size. It also seems probable that the difference in rate is not due to any difference in the initial stimulus of the operation, for the new growth at the two levels is more nearly the same at first than it is later. So much for what the difference is not; and in this list we may seem to have exhausted nearly all of the *physiological* possibilities in the ordinary sense of that term. The results seem comparable in many ways with the results of normal growth. A young animal grows rapidly at first, later more slowly as the adult form is approached. The same thing happens with the regenerated part. In both cases some inhibition takes place when a certain form or size is attained. Before discussing this point further let us consider more in detail some further facts about the earthworm which give a better basis for the discussion that will follow.

When the posterior end is cut off near the tip of the tail, regeneration of a new tip goes on with great slowness. When the worm is cut in two near the middle of the body, the regeneration of the posterior end takes place much more rapidly than in the last case. If even more of the posterior part is removed, the missing part is regenerated somewhat faster than when cut in the middle. On the other hand, when the anterior end of a worm is cut off, the results appear to be different, but in reality the difference is more apparent than real. When one, two, three, four, or five anterior segments are cut off, the same number that was removed comes back, as a rule; but when more than five are cut off, only five at most come back. In these cases all the new segments are laid down at once, and no more are formed later. In the tail region the new terminal part is also laid down for all levels at about the same time, but a growing region is formed near the end, and from this the new segments are added. It is in this terminal growth, characteristic of the posterior end alone, that the difference in the rate of growth is found.

It can be shown, I think, with some probability, that we have to deal in these cases with more than a single factor. In the first place, the kind of differentiation at each level may determine not

only the kind of new organ that is produced, but to some extent the rate with which the new part makes its *first* appearance. For example, in the earthworm a new head will develop only as far back as the 15th to the 18th segment. Behind that level a reversed tail develops from the anterior end of the piece. The simplest explanation of this is, I think, that the differentiated material of the head has so far diminished when this level is reached, and the differentiated material of a tail is so much in excess, that a tail and not a head is formed. In the region of the 15th to the 18th segment a head sometimes develops, but it is always imperfect. Conversely, a posterior end will not develop from a posterior cut surface farther forward than about the 12th to the 15th segment. Here, also, we may assume that the head material has so much increased that a new tail no longer develops. But this explanation will not account for the different rates of development of a tail at different levels, unless we assume that there is more of the tail-differentiated material in the region anterior to the middle of the worm, which is inconsistent with the preceding assumption of the distribution of the materials. Moreover, even if this were the case the assumption would not explain the facts, for a new tail, that is derived from the material at the middle of the worm, also grows more slowly as it reaches the termination of its length.

Other factors, therefore, must be postulated to account for the difference in the rate of growth at different levels. Two such factors may possibly be recognized. In the first place when a new part is first laid down in the newly proliferated material the terminal part is the first formed, and as much of it is produced as the proportions of the new part allow. For instance, when more than five segments are removed from the anterior end of the earthworm only the five distal segments at most are formed; and since no growing region is produced between the old and the new part, or in the new part itself (since a growing region is not characteristic of the anterior end), no more than five segments are ever produced. When the posterior end of the worm is cut off there is also formed at first the

distal end, but this is characterized by the presence of a growing region, which continues to add new segments to the new part.

What factor determines that the *terminal* organs are those that are first laid down in the new part? It cannot be the shape of the new part as such, for this is practically a dome-shaped knob for all new parts. The bounding surface seems certainly to be a factor in this relation of the parts, as does also the relation of the old organs or layers at the cut surface. Between these two boundaries the relation of the parts to each other determines the result. A number of considerations, that I cannot enter into more fully here, have led me to suspect that this relation of the parts can be accounted for as due to a condition of stratification or polarity, due to the mutual pressure of the parts on each other, which acts as the stimulus for the differentiation of the cells. By these same assumptions we can, I think, also give a fairly consistent explanation of the difference in the rate of growth at different levels.

Let us take, by way of illustration, the results that have been obtained in another worm, lumbriculus. If the worm is cut in two at almost any level, there develops from the posterior end of the anterior piece a new tail, and from the anterior end of the posterior piece a new head. The material out of which these two new parts develop must be identical. What determines, then, that the new material forms in one case a head and in the other a tail? Since the development of these new parts seems to be largely a centripetal phenomenon, we cannot assume that the influence of the old part on the new, a centrifugal influence, determines the result; but since the order or sequence of the differentiation in the new part is the same as that in the old part, this may determine whether a head or a tail develops. In other words, the polarity of the new part is in each case the same as that of the old. This polarity is an expression of the stratification of the differentiation; at least, this is the most probable view of polarity, I think, that we can find at present. The centripetal influence acting on the new material at the anterior end determines therefore that

this is a head, and acting on the new material at the posterior end determines that this is a tail. The centripetal influence is, according to my interpretation, nothing more than the tension of the outer layer of cells, and the pressure relations in general, in the rounded dome-shaped mass of new materials. In this way we can give a formal solution of the development of a head in one case and of a tail in the other.

Let us see whether the same hypothesis will explain the different rates of growth of the posterior end according to the level of the cut, as seen in the earthworm, salamander, and fish. A growing region is present near, but not quite at, the tip of the tail. From this region new material is continually being produced, out of which the new part is differentiated. The way in which this new part differentiates is determined by the pressure relation of the neighboring parts. This pressure relation is the result of the differentiation, with its concomitant pressure relations, that has already taken place in the old part on the one side, and of the tension of the new material of the tip on the other side. The new part differentiates therefore into something that is less than the former and more than the latter. In consequence there will be an ever decreasing stimulus and differentiation as the new parts are formed, until finally no further stimulus for growth and differentiation is present or is strong enough to act, and the growth comes to an end.

In some such way as this we can, provisionally at least, account for the difference in rate at different levels, since the rate is determined by the pressure relations of the different parts, and this pressure decreases as a stimulus from the middle toward the posterior end. In principle this assumption refers the changes that take place to a formative factor or factors. It assumes that the differentiation *for a given material* is a response to pressure relations. The nature of response is unknown, as in all other cases where living material responds to external conditions, but that living material possesses a power to respond by differentiating to external agents, and even to pressure relations, is too well known to require demonstration. We are deal-

ing here, no doubt, with an extremely elusive and difficult problem, but one that is of fundamental importance in all questions in which the problem of organic form appears. It may be that there are factors at work here of which as yet we have little real conception, and any such attempt as this that I have made to give the facts an explanation on more or less familiar assumptions may be premature. I hope, nevertheless, that I may have succeeded in calling attention to certain important phenomena of growth, and even if my attempt to bring the results under one point of view should prove unsatisfactory, the attempt may at least serve as a suggestion for further work along these lines.

To sum up: I have attempted to account for certain phenomena of regeneration by a process of growth in which the following factors appear to enter: (1) the differentiated material as a factor in limiting the character of new parts; (2) the relation of the cells to each other as a factor in their differentiation, and assume that this relation is due to the mutual pressures or tensions of the cells on each other; (3) the differentiated cells also determine the existing tension in that part, and this may in turn react on the new cells with which they are in contact. Remove a part and the pressure relations are upset, but this leads ultimately to the reëstablishment again of the same relations of pressure.

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EXPERIMENTAL STUDIES IN GRAFTING

CHAPTER XVIII

EXPERIMENTS IN GRAFTING

ALTHOUGH the process of grafting has long been carried out by horticulturists for practical purposes, it is only within recent years that the process has been extensively used with animals in order to study certain scientific problems.

Trembley's experiments in grafting hydra, carried out in 1744, are the first, so far as I know, recorded for animals. Later Hunter and Duhamel grafted the spur of a cock on the comb, where it continued to grow. The experiment is interesting only on account of the bizarre nature of the combination.

The method of grafting carried out with plants is different from that practiced with animals in one essential respect; namely, that while in plants small buds are inserted in the stock, in animals the cut ends of fully formed structures are united, and this may sometimes involve the union of cross-sections of the entire animal.

A number of important questions are involved in the results of grafting. The main topics to be considered here fall under four headings: (1) the facility with which different regions can be united; (2) the influence of united parts on each other; (3) the possibility of hybridizing by grafting; (4) special problems of embryonic development as studied by means of grafting.

The Union of Different Regions

The simplest kind of union is that where a part of an animal is cut off and put back in place, as when a limb is cut off and grafted again in the same position, or as when a worm is cut in two and the two parts (complementary parts) are reunited.

A step further involves the union of different regions, and many combinations of this sort have been made. It is a point of some interest to find that complementary parts unite with no greater facility than unlike parts, and even parts with reversed orientation unite as readily as do those having the same orientation.

A series of important experiments in grafting earthworms have been made by Joest. The cut surfaces are held together by means of two or three ligatures through the skin. In the course of a few days the contact surfaces unite with each other, and the threads are sloughed off. Parts of different individuals can be united as readily as parts of the same worm. Not only complementary regions can be united, but cut surfaces of different levels, and in this way short or long combinations can be made. For instance, if the middle region of a worm is cut out, and the end pieces grafted together, a "short" worm is produced. If the union is perfect, no regeneration takes place where the pieces have grown together. It also appears that the tail end of the short worm does not continue to grow to make the worm longer. A "long" worm may be made by inserting a middle piece between the anterior and posterior halves of another worm. This combination is also permanent, if the parts have been perfectly united.

In the preceding cases a posterior cut surface is united to an anterior cut surface, *i.e.* the pieces have the same orientation. It is possible also to unite two anterior cut surfaces or two posterior cut surfaces. For example, if two tail ends of two worms are sewed together by their anterior cut surfaces, a permanent union may be effected without subsequent regeneration, although the combination has two tails and no head, and must slowly starve to death. It is more difficult to unite two posterior cut surfaces, not because of any inherent difficulty in the growing together of the parts, but because the pieces tend to crawl away from each other, and break the ligatures before union of the tissues has been effected.

The results are somewhat different if the cut surfaces are brought together so that the median plane of one piece does not

correspond with that of the other. If, for instance, the nervous system of one piece is not opposite the nervous system of the other piece, regeneration at the place of union may subsequently occur. The nervous system is the most important factor in the result; for it acts as a center for the formation of the new part, which may be a head or a tail, or two heads, etc., according to the region that regenerates at the union. In some cases where the cut ends of the nervous system are not exactly opposite they find each other, and become united by a connective of nerve tissue, derived from the ectoderm of the region of union. The further the cut ends of the nervous cord are apart, the less likely are they to unite, and regeneration from one or from both cut ends is more likely to take place.

Born has shown that cut surfaces of very young tadpoles may be united, and he has made a great variety of combinations of these embryos. The method of grafting is very simple. The tadpoles are taken from the jelly capsules, cut in two with a sharp knife, and the cut ends quickly brought in contact with each other. The pieces are held in place by means of small blocks of silver.[1] The combinations are permanent, and in no case does regeneration take place from the cut surface even when like organs are not united. The tail region of one animal has been united to various parts of the body of another animal, where it remains attached and continues to develop, producing its normal structures. In one case, the tail grafted upon the ventral surface of another individual showed signs of being absorbed at the time of metamorphosis, when the normal tail was absorbed.

These results of grafting pieces upon parts of the body, different from those with which the part in question is continuous under normal conditions, show that the development of the part is due to self-differentiation, and that its development is not dependent on relation of the part to the rest of the organism.

Parts of planarians have been grafted together by Mrs. Mor-

[1] I have found that bent pieces of aluminium wire and short straight pieces of the same wire cut off very obliquely can be used to hold the pieces together.

gan. The principal results are those with Phagocata gracilis and Planaria maculata. Owing to the delicacy of the tissues and the mobility of the pieces a special method of holding the parts together has to be used. By placing the pieces to be united between wet sheets of very thin paper, they can be brought into close contact and kept in place by means of pieces of glass at the sides and needles at the ends. After several hours the pieces grow together. It has been found possible to unite cut surface from all different levels of the body. If the union is perfect and if the pieces are of the same size so that no free edges are left, the combination is permanent and regeneration does not take place at the cut surface. If the union is not perfect, regeneration may take place at the line of union. In this instance also it appears that when the cut ends of the nerve cords unite, regeneration at the line of graft does not occur; but if one or both of the nerve cords is free in either piece, one or two heads may appear. Especially interesting in this connection are the cases in which one of the pieces is turned upside down. This sort of union was made in several cases where the pieces were united by their anterior ends. Two heads regenerated at the line of graft, one above, the other below. Each was connected with the ventral nerve cord of one piece, and the distribution of pigment in the new heads showed that each head was made up on one surface of the material derived from one worm and on the other surface of material from the other worm.

Trembley first discovered that pieces of hydra could readily be grafted by simply bringing the cut surfaces together for a few minutes. It has been possible to make practically all kinds of unions, including pieces grafted in the side of another individual. As these results will be described in some detail in the next section, further description may be omitted here.

Another hydroid, Tubularia, has also been used for grafting experiments. Miss Peebles has shown that cut ends of the stalk readily unite if simply held together for a minute or two. In some cases no regeneration takes place at the line of graft, especially if regeneration takes place elsewhere, or in the vicinity

from a free end, but at other times one or two hydranths may develop near the region of union.

Crampton has carried out the ingenious experiment of uniting halves and portions of the pupæ of moths. After bringing the cut surfaces together they are held in place by melted paraffin placed around the line of union. The parts stick together and moths may emerge united in different ways according to the combinations formed at the time of union. The internal organs do not unite, and the union is incomplete in this respect, since, although sticking together, there is no continuity between the internal organs, but the skin and the integumentary organs in general do unite.

The preceding cases relate to combinations where large parts of the animals have been united. It has been long known in surgery that small pieces of different organs can be transplanted, and it is a regular practice to graft pieces of skin over exposed surfaces. These pieces of skin become attached, and their epithelial cells may spread over the exposed parts. Leo Loeb has found in the case of guinea pigs that black skin can be permanently established in the midst of a region of white skin, but white skin grafted upon a surface formerly occupied by black skin is slowly thrown off and replaced by black skin.

Ribbert has carried out many experiments in which pieces of different organs were grafted in foreign parts of the body. If these pieces are very small, they may remain alive for a long time, and even begin to proliferate new material. Subsequently, however, they become absorbed.

The Influence of the United Parts on Each Other: Formative Factors

In the cases given in the preceding section, with the exception of hydra and of the planarians, there is no attempt on the part of the united pieces to produce a new whole organism by a remodeling of the old parts. The case is different with hydra and planarians, especially the former, in which a process of remodeling or morphallaxis takes place in case the union does

not produce the typical form, so that a new whole of the characteristic type results. The difference in these two classes of cases is due to the different kinds of regenerative changes of which the animals are capable. Pieces of hydra and of planarians can transform themselves into the typical form with very little production of new tissue, and it is owing to this power that the changes about to be described are due. In the other animals, the tissues, when once formed, cannot remodel themselves into a new whole. At most they can only replace lost parts by first proliferating new material at the cut surface. The experiments to be described are the results of the work of Trembley, Wetzel, King, Rand, Peebles, and others.

When the anterior half of a hydra is grafted to the posterior half of a hydra, a single individual of normal proportions results, and no further changes take place (Fig. 21); but the result is different if the united pieces are shorter or longer than a normal hydra. If the anterior piece is less than half and the posterior piece is less than half, a short hydra is produced (Fig. 2). In this case the combination grows longer from day to day until the normal proportions are reached and a hydra of typical form results. If, on the other hand, both the anterior and the posterior pieces are each more than a half, a "long" hydra results (Fig. 3). The only way in which such an animal could become normal in length would be by the absorption of some of its parts, but it appears that hydra does not follow this method of remodeling. Instead it regenerates at the line of union a new foot that belongs to the anterior part, and new tentacles at the line of union that belong to the posterior part (Fig. 4). The two parts pinch in two between the new foot and the new tentacles, and two hydras result. Evidently the conditions in a "short" hydra and in a "long" hydra are different, since different results follow. In both cases we must suppose that the union between the cut ends is perfect, so that the result depends on some other relation in this region than imperfect union. The most plausible explanation is found, I think, in the adjustments of the pressure or tension relations of the united pieces. In a "short" hydra

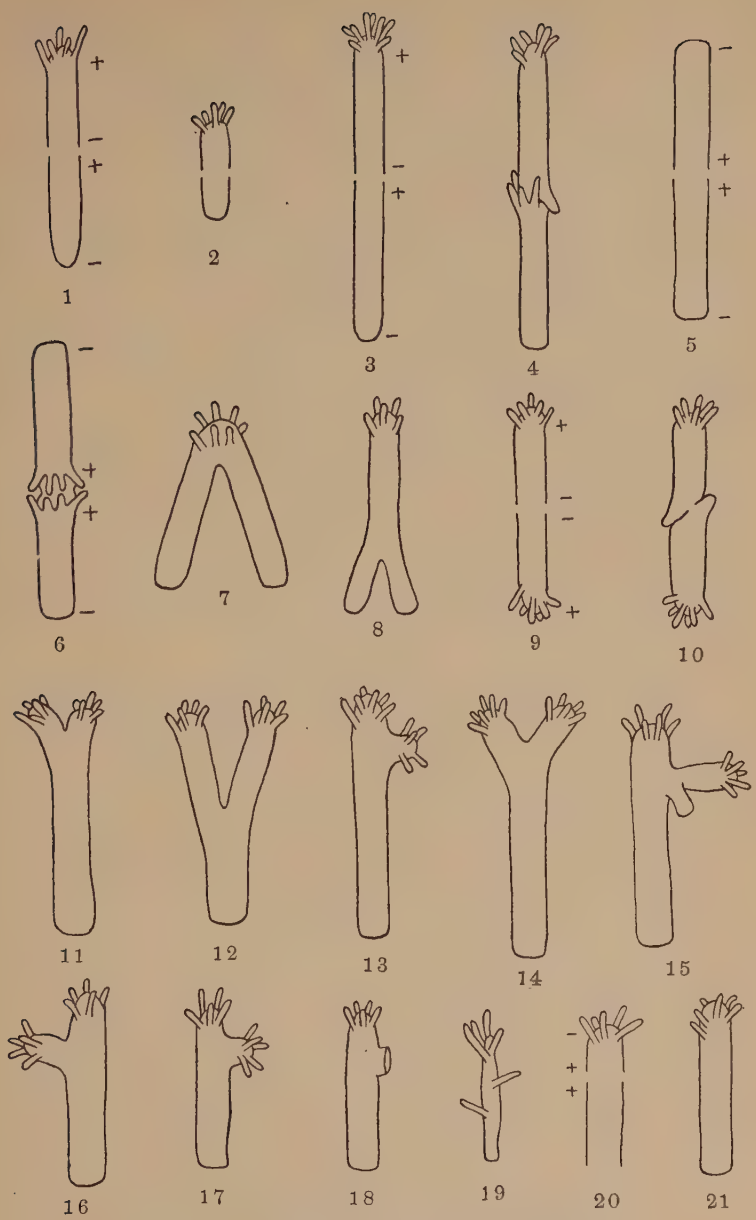

FIG. 21. Grafting in Hydra. For details, see text.

the united parts continue to change their form, in the same way as do separate pieces, until the relation of the parts of the cut surfaces is the same as that for the normal in this region, when further adjustment ceases. In the "long" hydra the same kind of changes take place, but the only way in which the typical relations could be adjusted would be either by absorbing the excessive parts, or by each piece, acting independently, assuming the typical form. The latter method is the one followed. This attempt to account for the different behavior of the two grafts may appear to be little more than a restatement of the facts; but if the restatement is correct, it has at least the advantage of referring the results to the factors that are operating. The hypothesis also involves a principle that will account for the other formative changes to be described.

If two pieces of hydra are united to each other by their anterior cut surfaces (Fig. 5), tentacles soon appear around one or both pieces near the line of union. If each half develops tentacles, the halves may pinch apart in the intermediate region (Fig. 6); if only one set of tentacles develops, a mouth may form, and the two pieces have a single crown of tentacles. Little by little the two pieces fuse together lengthwise into a single body as shown in Figs. 7 and 8, until finally one hydra results. The development of the tentacles at the line of union may possibly be accounted for by the inability of each piece to adjust its tension relations to the other; for although when halves are united in opposite directions the tension at the place of contact is the same as in the normal, since like regions are united, the reversal of the direction of the tensions in the opposed pieces makes it impossible for further relations to become established except by each part behaving as a separate individual. Here we meet with the conception of polarity as involved in the pressure relations. The polarity from this point of view is an expression of the graded pressure relations from one end of an organism to the other, which in turn may be an expression of the gradation of the tissues, and in turn may itself, under certain conditions, be the cause of the differentiation.

When two cut aboral ends are united (Fig. 9), two new foot processes are formed (Fig. 10), and the two pieces subsequently pinch apart to form each a separate individual. The explanation is the same as in the last case.

These results can be somewhat better understood when taken in connection with the experiments of hydras partially split lengthwise. If the anterior end is split for only a short distance, each half will round up and produce a separate head (Fig. 11). Subsequently the two heads may slowly fuse into a single one. The result is similar to the fusion of two bodies in the grafted hydra with one head. If the split extends farther into the hydra, as in Fig. 12, the two parts slowly draw apart until they finally pinch off at the foot region and produce two hydras. Why in one case the two separated parts unite and in the other case separate farther can possibly be explained on the view that I have tentatively suggested above. It will be noted that in the case of slightly separated heads the influence of the single body prevails, and reunites the parts from behind forward by drawing them together and establishing the normal tension relations; and in the case of the more separated anterior ends, these ends prevail and cause the single trunk to pinch farther apart, causing, as it were, the halves of the single trunk to draw up into their respective anterior ends.

The results of uniting the squarely cut posterior end of one individual with a cut surface in the side of another individual (Fig. 13) are similar in many ways to the last. The united pieces usually adjust themselves in such a way as to share the common trunk (Fig. 14). Subsequently the two pieces split apart farther and separate in the region of the foot. If the grafted piece does not succeed in halving the trunk, *i.e.* if it does not turn anteriorly, a foot develops at the line of union (Fig. 15), and the graft pinches off without passing down to the base of the stock. What conditions lead to this difference in behavior have not been sufficiently made out, but it is probable that the kind of union, or the relative sizes of the graft and

stock, or the likeness or unlikeness of the united levels, may account for the results.

A third possibility also exists in grafts made in this way. The graft itself may swing around into line with the trunk of the stock, and become the head of the new hydra (Fig. 16). The head of the stock shifts down to the base and there pinches off to produce a new hydra, leaving its original posterior end in the possession of the new head.

If a very short piece of the anterior end is grafted near the head of another hydra (Fig. 17), the two heads fuse into one. At first there are too many tentacles, but some of these are absorbed or even two tentacles fuse into a single one — a process not uncommon in hydra, producing, while in process of completion, the forked tentacles not infrequently found.

If the cut end of a hydra is grafted into the side of another hydra, and then, after union, the graft be cut off close to the stock (Fig. 18), the small ring (whose outer end closes) will be slowly absorbed into the stock. The result may be expressed in terms of my hypothesis as follows: The resistance in the cells of the small piece is insufficient to allow the piece to pinch off, and it is too different to permit it at first to share the common trunk. Not being able to free itself, and unable to maintain itself under unfavorable conditions of tension, it is absorbed, or changed over into a part of the body wall, the process being very slow as a rule.

It has been found[1] that different species of hydra behave somewhat differently. In Hydra fusca, lateral grafts tend to move forward until the head end is of the same length as that of the stock when fusion begins and unites the two parts. If, however, the lateral graft is inserted less than one fifth the distance from the lower end, it moves downward and constricts off at the base. In Hydra viridis, lateral grafts tend to move downward wherever united to the stock, and separate at the foot, unless inserted very near the head end of the stock, when the two heads fuse.

[1] Hefferan (1902).

In grafting or in splitting individuals, tentacles are sometimes displaced from their normal position, and may come to lie at some distance from the oral end. This result may easily be obtained by cutting off the head just below the line of the tentacles. When the new trunk is formed individual tentacles often become drawn out of place (Fig. 19). In all these cases the tentacles become absorbed after a time. The result is important, because the special conditions in the case of hydra preclude, with much probability, the explanation of the absorption as due to food relations. The tentacles are hollow and open directly into the central digestive space. A tentacle attached at the side is situated in as favorable a place for receiving food as are those of the ring, yet it is absorbed. The result is similar to the absorption of small grafts in the same position, and the explanation of the absorption is probably the same in both cases.

One of the most important results obtained by grafting hydra is the reversal of polarity that can be brought about in the following way: If two pieces are united by their anterior or oral ends, and then one of them is cut off near the line of union (Fig. 20), it will often produce, if very short, a mouth and tentacles (head) from its exposed aboral or posterior end (Fig. 21). Thus instead of a foot a head develops. This result occurs only when the piece is very short. It seems that the polarity has been reversed, owing to the union with a larger piece. The result is difficult to explain; possibly the conditions of tension may actually be changed in the smaller piece through the influence of the larger piece, so that the orientation is reversed. The experiment needs very careful reëxamination before we can safely offer a probable explanation of the result.

The planarians are also capable of remodeling the proportions of the old parts to produce a new worm of typical proportions. In this case, however, the new head and tail are formed in proliferated material, but the rest of the body is remodeled. Abnormally placed parts, resulting from grafting or from cutting, do not show the power of pinching apart exhibited by hydra, but may after a time be absorbed, especially if small and not sup-

plied with a mouth opening. The reversal of polarity described for reversed grafts of hydra has been discovered by Mrs. Morgan to take place in planarians also when the piece is very short. If, for instance, anterior cut surfaces of two pieces are united, and one of the pieces is subsequently cut off near the line of union, that piece if very short produces a head at its posterior exposed end. Here also it appears that the results may be due to the influence of the old part. In this case there is no question of absorption of the smaller piece, but there is on the other hand ample opportunity for inwandering cells to pass from the large part through the small piece into the new material. The result is further complicated by the fact that very short pieces of other species of planarians, that are not grafted, may produce a head at the anterior end and another at the posterior end, and while at present this result has not been obtained with Plagocata, the possibility still exists that the results may be due to the cut-off pieces that have been tested for double heads being somewhat longer than the small grafted piece in the reversed position. If the grafted piece is longer, it produces a tail at its posterior end and not a head.

Miss Peebles has shown in Tubularia that small pieces grafted on to the ends of large pieces may sometimes take part in producing the single head that develops. This may occur also when the small piece is reversed in direction; but it cannot be shown in this case that the reversed head is due to its union with the larger piece, because Tubularia produces a new head so readily from either the aboral or oral end that even if some influence of the larger piece exists it would be difficult to prove.

The peculiar power of pieces of hydra, planarians, etc., to mold themselves into a new form of typical proportions is clearly similar to the molding that takes place in embryonic development. The older writers used the term "formative force" to account for this power to undergo changes in form, but modern investigators avoid the use of this term, because no such form of energy is known in the physical world; and because we should have to postulate as many kinds of formative forces to

explain the results as there are different species of animals having this power. In other words, the use of the term "formative force" is only a restatement of the problem, not a causal explanation of it. Perhaps the main objection to this, and to similar terms, is that they imply the existence in living matter of forces, or energies, or factors that are not exhibited by non-living things. In so far as there is postulated only a different kind of physical action from any so far described by physicists, little objection can be raised; but until the nature of this new force can be demonstrated, very little if anything is gained by assuming its existence. If, on the other hand, the postulated principle is supposed to be different in character from all other physical events, then the matter becomes more serious; for the assumption is either metaphysical, and therefore outside of the proper field of science, or if not metaphysical, the assumption attempts to account for known events by a principle entirely unknown. In the latter case nothing is gained, and since the nature of the question itself is prejudged, harm may be done. In the preceding pages, in attempting to account for the changes in hydra, etc., I have assumed that the formative changes are the outcome of a relation of tension in the parts. From this point of view the condition of tension is the stimulus to which the material basis of the organism responds.

The postulated factor is a physical one, and the response of the cells that determines the result is supposed to be, in most cases, the familiar response of contraction shown by all animals. In this respect the nature of the process is assumed to be the same as that seen in other phenomena involving contact and response by contraction. There is nothing in the nature of this reaction that seems to preclude a purely physical process. In addition, however, it is necessary to assume that the differentiation of the cells also takes place as a result of the mutual pressure of the parts on each other. This assumption is more arbitrary and more difficult to bring into accord with our present knowledge; yet the facts seem to demand, I think, some such view, although at present it can only be offered as a provisional or working hypothesis.

The Union of Parts of Different Species

As Darwin long ago pointed out, the union of parts of different species has many points in common with the fertilization of the egg of one species with the sperm of the other. In both cases the combination can sometimes be successfully made, while in others it cannot. Furthermore, the general statement may be made for both cases that closely related species combine more readily than those far apart, *i.e.* the results are more successful for unions between closely "related" forms than between distantly "related" forms. Certain exceptions exist, however, in both directions.

The principal experiments with animals are those of Joest with earthworms; of Born with tadpoles; and of Wetzel with hydra.

It has been found to be more difficult to unite pieces of different species of earthworms than of the same species; nevertheless Joest has succeeded in making a number of combinations of different species. The most successful union, *i.e.* the one that was most easily made, is that between Lumbricus rubellus and Allolobophora terrestris. A compound worm of this sort lived for eight months. Neither part showed any material influence of the other half, although the blood circulating through the worm went from one to the other. It may appear, in this case, that since both parts were completely formed at the time of union, there is given no chance for the influence of the parts on each other to manifest itself. If, however, a part of one of the components is removed and a new part regenerates, the new part must derive its nourishment from the materials in the blood that come from both components. The possibility of such an influence was tested in a compound made up of Lumbricus rubellus and Allolobophora fœtida. The new head regenerated from Lumbricus rubellus, that is the lighter in color. It was of the same color as L. rubellus, and showed no influence of the darker color of the other component, A. terrestris.

Born has also found that it is more difficult to get pieces of

different species of tadpoles to unite than pieces of the same species, although Rana esculenta can be united with ease to Rana fusca or to R. arvalis. The facility with which the pieces unite is owing to the rapidity with which the ectoderm of Rana esculenta covers exposed surfaces. Rana fusca and R. arvalis do not combine so readily, because the ectoderm unites very slowly. On the other hand, it is very easy to unite Rana esculenta with Bufo igneus, but not permanently, as the parts die or separate. In one case, however, the union lasted for three weeks. Partial union, but of short duration, was effected between the tadpole of Rana esculenta and a larval Triton.

Although some of these combinations between different species lasted for some time, and seemed to be permanent in several cases, each part developed only its own specific peculiarities, as seen especially in the color. No hybridizing effects were apparent.

Harrison has united the anterior half of Rana virescens to the posterior half of Rana palustris, and has reared young frogs from the combination. The anterior half of the body of these frogs showed the characters of one species and the posterior part that of the other. There was no trace of mutual influence between the two halves.

I have examined a case in which the relation of the parts is so intimate that were there any influence exerted we should expect to get evidence of it. The tip of the tail of a young tadpole of Rana sylvatica was united to the tail of Rana palustris (from which previously an equivalent piece had been removed) (Fig. 22, B). As the new tail grows out, the dark ectoderm of R. sylvatica is carried out to the tip (Fig. C), while the underlying cells remain behind, and come to be covered over by the light yellow ectoderm of R. palustris. If now the tail is cut off at the line indicated by the vertical line *a–a*, this cut end will be made up of the inner organs of R. sylvatica, and, externally, of the skin of R. palustris. When the new tail regenerates (Fig. E) the opportunity for mutual influence of the parts is afforded, yet no such influence was apparent. Other experiments of a

similar kind gave the same result. Especially instructive is the case where the new ectoderm is derived partly from one component, partly from the other species (as when the tail is cut off as shown at *b–b* in Fig. C). No influence of the ecto-

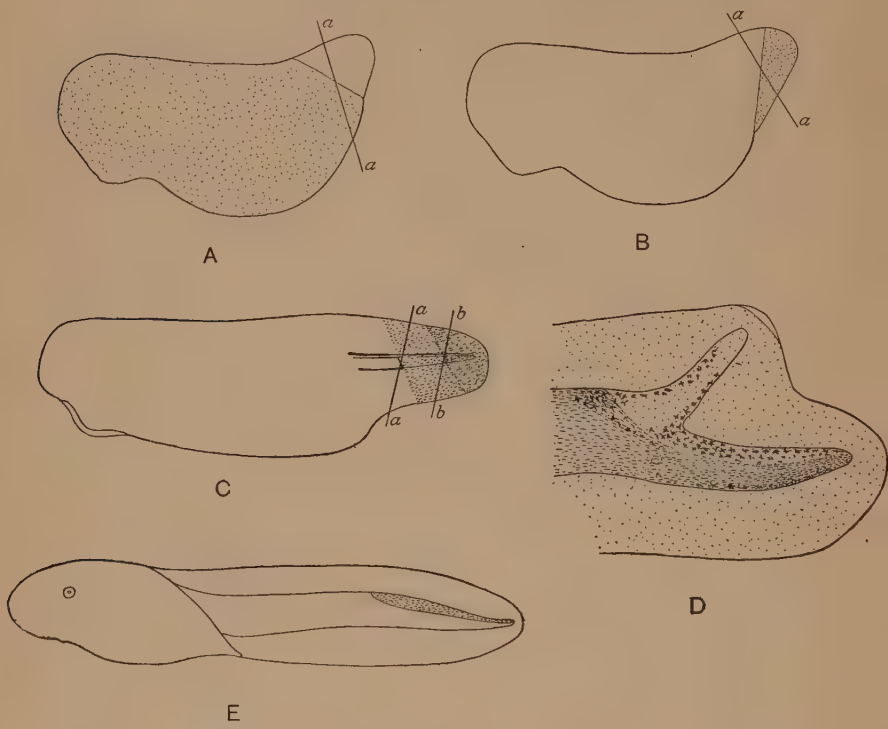

Fig. 22. Grafted tail of frog. Fig. A, Rana sylvatica with grafted tail of Rana palustris. Fig. B, reciprocal graft. Fig. C, late stage of last. Fig. D, newly regenerated tail of Fig. A cut off at *a–a*. Fig. E, newly regenerated tail of Fig. C cut off at *a–a*.

derm cells on each other could be detected, although they are in intimate contact.

The attempt to unite pieces of brown hydra, H. fusca, to pieces of green hydra, H. viridis, has not succeeded. Wetzel has shown that although the two pieces will stick together for a few hours, or even days, they subsequently separate; but the union of Hydra fusca and H. grisca was successfully carried out.

Crampton has studied the effects of uniting parts of different species of moths. The pupæ of the species to be united were cut across, and the exposed surfaces brought into contact and held in place by a coating of paraffin. In successful cases the parts united, at least so far as the integumentary organs are concerned, and the moths that subsequently emerged were made up of parts of two species. As a rule, each part developed its own specific coloring, showing no mutual influence of the parts on each other. In two cases, however, evidence of some influence was found. The posterior part of the abdomen of a female pupa of Callosamia promethea was united to the rest of the body of Samia cecropia. In the moth the *promethea* part assumed the color of the *cecropia*. In another union between Telea polyphemus and Samia cecropia the small piece of the latter assumed the color of the former. According to Mayer, the color in these moths is largely due to the drying of the hæmalymph. The explanation of the two cases just given may be that some of the hæmalymph of the larger component got into the smaller part. If the result is due to this, the outcome is only remotely connected with the "influence" of one part on another.

In conclusion, it is apparent that grafted pieces of different species have no mutual influence on each other of the kind that characterizes species. In this respect the results are quite different from the effects of cross-fertilization; the difference is probably due to the actual union within the same cell of the characters of the two parents in cross-fertilization, and to the absence of any such intimate fusion in the case of grafting. In other words the cells retain their specific characters in the unions by grafting, and although cells of different species may live side by side and form a part of a new individual, they have no influence of a specific nature on each other.

Special Problems of Development

It has been pointed out that by means of grafting it has been found possible to study the question of self-development *versus* correlated development of parts of the embryo. In most cases

it has been found that after the development and differentiation of a part have begun it continues to self-differentiate even if removed to another part of the embryo. As an example of correlated development, an experiment carried out by Lewis may be cited.

Lewis has shown that any part of the ectoderm of the embryo of the frog can produce the lens of the eye, provided a piece of the optic vesicle is transplanted beneath it. The result shows that the optic vesicle exerts a formative stimulus on the ectoderm, calling forth the lens formation. This case is the best-ascertained example of the so-called formative stimulus and one of the few indisputable cases of the sort. Although embryologists have some reason to conclude that similar stimuli may play an important rôle in development, it has been found difficult to obtain evidence of this kind of action. On the other hand, the power of independent self-differentiation of the parts has been demonstrated in a large number of cases. Both principles appear to play a rôle in the development of the embryo.

In a somewhat different way Lewis has examined the same problem. He removed the ectoderm lying over the eye vesicle and transplanted there a piece from another animal — a different species, in fact, whose skin was differently colored. The lens developed at the proper time from the grafted piece.

In contrast to these results Lewis found that pieces of the eye vesicle transplanted in different parts of the body underwent there self-development and differentiation.

Harrison has studied the perplexing problem of the normal growth of the nerves in the embryo, by uniting parts of the bodies of young tadpoles in such a way that the nerve must extend into a territory that is normally foreign to that nerve. Since the nerve extends into the new region, Harrison concluded that its growth takes place by its own substance extending outward, and not by the addition of cells in the new part.

Braus has recently studied the same problem in another way. The limb bud of the tadpole, at a very early stage in its develop-

ment, was extirpated and grafted on another part of the body. At the time of removal he believed that the nerves had not extended into the region of the limb. The bud developed in its new location into a complete structure possessing the normal nerves, which were larger than the body nerves with which they were found to be connected. Braus concluded that the nerves of the limbs do not grow out from the spinal cord, as His and his followers claim, but differentiate in the limb itself.

In another experiment the problem has been examined in a different way. It had been shown by Harrison that if the dorsal part of the young embryo of the frog, including the nerve cord, be removed, the embryo may continue for a time to develop. Braus carried out this operation, and after the bud of the hind limb had appeared he removed it, and transplanted it upon another normal embryo. The bud developed into a normal limb, *except that it entirely lacked nerves.* In this respect it differed from the preceding case. It might appear that in the first case the nerves had already grown into the limb, hence their development when the limb was transplanted. This interpretation, Braus states, is negatived by two considerations: first, he could not find that the nerves had grown into the limb at the time of its removal; second, even if they had we should expect them to degenerate when removed from their central connections. Moreover, if nerves grew out from the central nervous system into the grafted limb, it is not evident why they should grow out in the first case given above and not in the present case. Braus interprets his results as follows: The peripheral nerves are formed out of the intercellular protoplasmic connections between the cells of the embryo. The stimulus that leads to their development into nerve bundles originates from the nerves that start from the central nervous system; hence the nerves themselves appear as though extensions of the nerve processes of the cells coming from the nerve cord. If the central nervous system is destroyed at an early stage, the time may pass by when the intercellular connections in the limb bud can respond to the central influence, hence the failure of such a limb bud to develop its nerves when

grafted upon another individual. On the other hand, the limb bud of a normal individual has already received its proper stimulus before its removal, hence the independent development in it of the peripheral nerves. While the argument is far from convincing,[1] yet the method gives promise of throwing light on a very difficult and obscure point.

There is another result of interest connected with these grafting experiments of Braus. He finds when the bud of the fore leg is grafted in another part of the body — near the hind leg, for example — that in the majority of cases two legs develop, — one at first more advanced than the other, and the more advanced leg alone contains nerves. In the light of some recent experiments of Tornier, in which four complete hind limbs of the frog are artificially induced by splitting the limb buds, there can be no doubt that the less advanced leg, in Braus's experiment, is a regenerative product. It fails to receive nerves either from its twin leg, of which it is a mirror figure, or from the main body of the tadpole, or at least no medullated nerves.

Aside from the interesting questions concerned in the formation of the nerves the experiments of Harrison and of Braus are important in showing that as complicated an organ as the leg of the frog may develop in the complete absence of peripheral nerves. The result shows, if true, that the self-differentiation of all the tissues of the leg may take place in the entire absence of connection by means of nerves with the central nervous system.

[1] The experiments of Braus have been repeated by Harrison upon frog and toad embryos, the result having been briefly reported at the Toronto meeting of the British Medical Association, August, 1906. Contrary to Braus, Harrison finds that nerves are present, after a time, in limbs developed from buds which are transplanted from "nerveless" embryos. These nerves have normal relation to the other structures in the limb, at least as far as the main features are concerned, though the finer details have not yet been studied. Furthermore, in cases where two limbs have developed out of a single transplanted bud, Harrison has found that nerves are present in both. Braus's results are probably to be explained by the fact that he did not keep his specimens alive for a sufficient length of time after the operation. Be this as it may, Harrison's experiments show beyond doubt that the nerves grow from the body of the host into the transplanted appendage, and also that it is the configuration of the organs and tissues in the appendage that determines the course taken by the outgrowing fibers.

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EXPERIMENTAL STUDIES OF THE INFLUENCE OF THE ENVIRONMENT ON THE LIFE-CYCLE

CHAPTER XIX

CHANGES IN THE LIFE-CYCLE AND CHANGES IN THE ENVIRONMENT

The Life Histories of Some Animals

In the life histories of many animals and plants a series of stages succeed each other until, with the completion of the cycle, the starting point is reached again. In some species the series of forms that make up the life-cycle seem to change without any change taking place in the environment, that remains the same throughout, but in other cases the change in the cycle is associated with a change in the environment. It is this latter class that we may now examine, although it will also be profitable not to neglect the other.

The life-cycle of most animals is made up of a single adult individual and a series of embryonic stages through which the embryo passes to become an adult. The cycle consists, therefore, of adult, egg (and sperm), embryo, larva, adult. In other cases the life-cycle is more complex, as it may contain more than one adult form and include several modes of reproduction.

In some species the cycle seems to complete itself under constant external conditions, as stated above, while in closely related groups the change appears to be connected with a change in the environment. For instance, many of the marine hydroids show an alternation of generations that does not appear to be directly connected with changes in their surroundings. The egg develops into a swimming embryo that settles down and becomes a polyp. The polyp produces buds, all of which are also polyps. This process continues until the colony has reached a certain stage, when a new kind of bud arises that becomes a jellyfish. The jellyfish detaches itself, and comes to lead an independent exist-

ence in the sea. This jellyfish produces eggs, and the egg after fertilization develops into the primary polyp, completing the cycle. The cycle is passed through during the summer, as a rule, in our northern waters, and there is nothing to indicate that external factors determine that a bud, developing later in the season, must become a jellyfish and not a polyp. We may suppose that differences in temperature or in the food supply bring about the change, but as yet there is no proof that this is the case. It would certainly be worth while to attempt to find out whether external conditions are factors in the result; but so far as we can see at present the jellyfish bud appears when the colony reaches a certain size. It should not be overlooked that this size is far from being fixed, and may vary in different colonies when the jellyfish are formed. The important consideration is that as the colony grows larger its relation to the environment must become different from what it was at first, so that even if the environment remains the same the animal enters into a different relation with it.

This point is well illustrated by certain recent experiments of Klebs. The flowering plants produce at first only leaves and branches. When they reach a certain size they produce flowers. Klebs points out that most botanists look upon the flowering of the plant as the culmination of its form. The form is something that perfects itself under favorable conditions without respect to the environment. Klebs, on the other hand, thinks that the development of the flowers is simply due to a relation that becomes established between the plant (when it attains a certain size or stage) and the external conditions, and he brings forward in support of his idea a number of confirmatory experiments. These show how by altering the conditions a shoot that would ordinarily develop into a flowering branch continues to grow vegetatively, producing only leaves.

In the green hydra the change from the non-sexual to the sexual mode of reproduction seems to be connected with definite seasons of the year, and possibly, therefore, with a change in the environment. Throughout the summer, the autumn, and

the winter the hydra produces buds that pinch off and become new individuals instead of remaining a part of the parent to form a colony. The size of hydra remains more or less constant. In the spring, sperm and eggs are produced. If the hydras are brought into a warm place in the autumn or in the winter, they will begin to produce sperm and eggs in a few weeks. This fact seems to indicate that the change produces the result; but whether this change is the effect of the cold, or of the warmth after the cold, or of both combined, or of some food relation, has not yet been made out.

Passing now to an examination of those cases where the changes in the life-cycle are known to be definitely connected with changes in the environment, I shall mention first the well-known case of the rose aphids or plant lice. These insects produce generation after generation of wingless,[1] parthenogenetic individuals throughout the summer. In the autumn a generation of winged males and wingless females appears. These pair and afterward the females deposit each a few "winter eggs" on the food plant. From these eggs the young parthenogenetic females hatch in the following spring and start the summer broods.

It has been shown for the rose aphid that if the parthenogenetic summer forms are brought into the greenhouse and put on roses, they will continue to produce parthenogenetic young, and the sexual forms never appear. Bonnet saw nine generations of parthenogenetic forms; Duval counted eleven in the course of seven months; Kyber kept aphids in a hothouse for four years and observed only parthenogenetic reproduction. It is evident, therefore, that if the external conditions are favorable, the non-sexual mode of reproduction may continue forever, as far as we can see. What, then, are the external conditions that determine the production of the sexual forms? The change occurs in the autumn when the cold weather begins to set in, and it may appear that the cold is the cause of the change. I have

[1] A few winged individuals appear in almost every generation, but these are not the sexual forms as has been sometimes supposed.

subjected roses with aphids on them to the cold of an ice box without producing any effect. Moreover, the sexual form may appear in the autumn before the cold weather has come. Even under ordinary conditions all of the aphids do not become sexual forms and hundreds of them perish by the frost. I have kept a potted rose out of doors for three months after the sexual forms had appeared, and yet those individuals that remained alive after this time continued to reproduce parthenogenetically. Finally, the individuals that seem to be less affected are those that are found on the growing tips of the branches, where the leaves are still young and succulent. These observations suggest that the change is not due to the cold, but to some changes in the food plant that take place in the autumn. Whether the result is due, as seems probable, to a lack of food, or to a reduction in the amount of water, or to both combined, remains to be shown.

A case apparently similar to that of the aphids is found in the Daphnians. These crustacea also produce parthenogenetically during the summer, and in the autumn the sexual forms appear. It has recently been shown by Issakowitsch that the change is probably due to a change in the food supply, and that the transformation can be quickly induced artificially by altering the external conditions. This and other cases will be given more fully in later chapters.

In the life histories of the ciliate infusoria, periods of division are succeeded by periods of conjugation. Maupas thought that after a long succession of divisions this mode of propagation comes slowly to an end, and that unless conjugation occurs the individuals will die. Immediately after conjugation, when division is very active, there is little tendency to conjugate again; but the longer the time elapsing after this process, the more prone are the individuals to unite in pairs, especially those of a different parentage. It would seem that an internal factor is here involved; but there are some indications that external factors may also enter into the result. It has been shown by Calkins that when paramœcium has undergone many divisions,

and the process appears to be reaching its limit, the individuals may be rejuvenated by altering the composition of the solution in which they live. They will then once more begin to divide actively and start a new cycle or a new phase of the old cycle. After a time under a constant environment their activity may again begin to fall off, when a new change may rejuvenate them once more. The precise effects produced are not known; for it has been found that a change that affects rejuvenescence at one time will not do so at another, and a different solution must be used. The conclusion seems near at hand that conjugation between individuals that have lived under different environments may effect the same result in the same way as a change in the environment itself. The problem may be, however, more complicated than this.

Influence of Food on the Life-cycle of Lepidoptera

The caterpillars of moths and butterflies undergo a series of moults as they grow larger, and during this time they consume a very large amount of food. The length of the larval life varies enormously. Thus according to Pictet the caterpillar of Argynnis paphia takes 15 to 20 days from egg to chrysalis. The caterpillars of the Vanessas take three to four weeks; Ocneria dispar and Saturnia pavonia two and a half to three months; Lasiocampa quercifolia eleven months (of which five are in hibernation); Cossus cossus holds the record with a larval life of two to three years.

The pupa or chrysalid stages also have various periods. Certain Vanessas take 12 to 18 days, and Ocneria dispar, Lasiocampa quercifolia, and Cossus cossus take 18 to 28 days. Saturnia pavonia and S. pyri that become inclosed in the spring generally pass two winters as chrysalids or pupæ. The length of life of these stages is, however, subject to great variation. The amount of food obtainable is an important element in the result.

Lasiocampa quercus hatches from the egg in the summer. The larva remains active till about the first of November, hibernates in the caterpillar stage until the end of April, when it

becomes active again with the return of vegetation, and becomes a chrysalid, emerging after a month in this condition in July or August, when the eggs are laid. If the caterpillars are kept in a warm place in the autumn and during the winter, they hibernate nevertheless, although the resting stage, the diapause, may be much affected. If the caterpillars are left outside in the cold for a while and then brought into the warmth, they awake a month sooner than normal, *i.e.* at the beginning of March, but nevertheless produce their typical moths at the normal time. Caterpillars that are not subjected to cold at all, but are brought into a warm room in the autumn, hibernate only a month, and begin in December their second period of activity preparatory to becoming a chrysalis, which occurs in March or April; but they do not emerge as moths until after an entire year, thus remaining chrysalids 13 months instead of only 28 days. The moth is identical with the normal. Thus by shortening the larval life the pupal life is prolonged.

Changes in food also affect the length of the different stages of development. For example, Ocneria dispar lays its eggs in July, and these do not hatch until the following April; the larval life extends to the middle of June; the pupa condition lasts until the middle of July. This is the normal course. Fed on the leaves of the walnut, the young caterpillars do not reach their complete development until the beginning of July, when they pupate, but the pupal life is correspondingly shortened and lasts only 20 days. Similar changes are affected by other plants that also supply insufficient nourishment. In all of these cases it was found that the larval life is prolonged and the pupal life shortened. The reverse effect is produced by those plants that furnish a better nutriment than the normal. The caterpillars grow rapidly and pupate 15 days sooner than do those fed on their habitual food plant, but the pupal life is sensibly prolonged. It lasts after Pimprenelle and Esparcette 40 days, after dandylion 43 days, instead of the ordinary 28 days. "What the insect gains in the larval stage it loses in the pupa stage."

Influence of the Environment on the Time of Ripening of the Sexual Organs

In most animals the sexual organs ripen their products when the adult form is reached, but in a few cases it has been shown that sexual maturity may obtain while the form of the body remains in the young or larval state. This phenomenon in its various forms has been called neotenia. The classical case is that of the axolotl. This salamander becomes sexually mature while still leading an aquatic life. It is a large, newt-like amphibian, eight to nine or even twelve inches in length. It has three pairs of branched external gills, a long tail with a dorsal and ventral fin. The animals were first found in the lakes near the City of Mexico. "For many years these creatures were looked upon as a species of Perennibranchiate, under the generic name of Siredon (S. axolotl, S. pisciformis, S. mexicanus, etc.), although Cuvier suspected that they were but the larvæ of an otherwise unknown terrestrial urodele. The mystery was not cleared up until the year 1865, when some axolotls, which had been kept for a year in the Jardin des Plantes at Paris, suddenly began to pair and laid eggs which within six months developed into full-sized axolotls. This certainly looked as if these creatures were not larval, but a true Perennibranchiate species. But to the general surprise several of these young Axolotls gradually lost their gills, the clefts closed up, the fins of the back and tail disappeared, the head became broader, the creatures left the water permanently, and in fact turned into the already well-known terrestrial Amblystoma tigrinum." [1]

It was this discovery that first gave the hint that the axolotl is a larval form.[2] At Weismann's suggestion Mlle. Marie v. Chauvin tried to bring about this change artificially, and succeeded in discovering the necessary conditions. The axolotls

[1] Gadow, H., "Amphibia and Reptiles," The Cambridge Natural History.

[2] It appears that other observers had already recorded similar conditions. Filippi in 1861 found tritons sexually mature but without the adult form, and Jullien found four female larvæ of Lissotriton punctatus with mature eggs, two of which were laid.

were first well fed so that they might be strong enough to pass through the period of metamorphosis during which they take no food; for if in poor condition they die before the transformation is completed. They were then put into shallow water, or on a moist surface, and in the course of one to three weeks, or longer, the change took place. The skin loses its sliminess, the dorsal fin disappears, the tail loses its broad border, and the gill slits close. The change appears to be connected with the enforced respiration by means of lungs instead of gills; possibly the drying of the skin may be a factor in the result.

Shufeldt[1] has given a very complete account of the metamorphosis of Amblystoma tigrinum in New Mexico. He finds that axolotls change into Amblystomas more readily if kept in water containing little air. If the transformation is induced to a certain point, the animal will complete it without further stimulus. Young axolotls are more easily made to transform than are older individuals. The metamorphosis is hastened by regularly supplying the animals with an abundance of food, "and what is still more interesting, when they are thus treated it markedly affects the appearance of the transformed Amblystomas." If well fed on meat the Amblystomas are not only larger, but of a deep black color without spots, while those not well fed are mottled with bright yellow and pale brown. The depth of the water seems to have "a wonderful influence" upon the metamorphosis; the deeper the water, the slower the metamorphosis.[2] A moderate increase in temperature seems to hasten the transformation. In the same pond in process of drying up all stages in the metamorphosis may be found, — animals caught in shallower parts undergoing a rapid transformation; those in deeper parts being unchanged.

Neotenia has also been observed in the tadpoles of frogs, but to a less degree, since they do not reach sexual maturity in this form. Certain organs, only, advance in their development, while others remain at an earlier stage. If the transformation of the

[1] *Science*, September, 1885, p. 263.

[2] This may possibly be due to the diminished chance of using the lungs.

tadpole is prevented by keeping the animals in cold water, the hind legs may continue to grow larger and their bones become harder. The long spiral intestine shortens, as it does when the tadpole changes into the frog, but the sexual organs do not mature.

How extensive the phenomenon of neotenia occurs in other amphibia is not known. It has been suggested that forms like Necturus, that always have external gills, do not represent more primitive members of the group, but are neotenic species that never undergo a metamorphosis, and become sexually mature in the larval stage. In other groups of the animal kingdom the same phenomenon occurs, according to some zoölogists. Thus it has been suggested that the rotifers represent the sexually mature trochophore larval stage of the annelids, which has lost its power to transform. Similarly, Appendicularia has been supposed to be a sexually mature larval form of an ascidian, and it has been suspected that even Amphioxus may be a neotenic form.

Boas has brought together many cases in which special organs remain in a lower stage of development, while other organs in the same animal undergo the characteristic transformation. Thus we seem to have three forms of neotenia: one in which the body remains at a lower stage and the sexual organs ripen; another in which some of the organs advance (as in the tadpole), but sexual maturity does not supervene; and third, those in which some organs fail to develop at the time of sexual maturity.

A case that appears to be a parallel one in some aspects exists in the white ants according to Grassi. The members of the colony consist of a royal couple, workers, soldiers, and young. If one of the royal pair is removed, a royal substitute form is reared, either male or female, according to which is needed. If both royal individuals are removed, two royal substitutes are reared. Grassi has shown experimentally that this occurs, but the way in which the transformation is effected was not determined, although he thinks that the amount or the kind of food given to the young determines the result. The young appear

at first to be all alike, and potentially have the power to become workers, soldiers, or substitute royal forms. The workers and the soldiers have rudimentary reproductive organs and are of both sexes. Their development is, in a sense, arrested, although they are something more than simply undeveloped individuals, since they have peculiarities that belong to their caste. The substitute royal forms are, however, according to Grassi, neotenic individuals in which the sexual organs develop, but the wings do not. In this and in some other respects they represent sexually mature larval forms. Although attempts have been made to discover the nature of the food that determines the fate of individuals of the colony, nothing definite has as yet been ascertained.

Grassi succeeded in establishing colonies in small glass tubes that could be carried about in his waistcoat pocket and studied through the walls of the tube. Colonies of from 15 to 40 individuals of different ages were thus established, made up of workers, soldiers, and young, but without sexual forms. After a few days, from two to six incipient substitute pairs appeared, characterized by pigmented eyes. In fact, Grassi says, even after 30 or 40 hours in summer he could tell which individuals would acquire the ocular pigment. The formation of these incipient royal substitutes does not take place if a royal pair is present; but if the king or the queen is removed for 24 or 48 hours, a few substitute forms begin to appear. In one case a nest was made up of only three large larvæ, and in two weeks one of these exhibited pigmented eyes, and was in process of becoming a substitute form. If a nest contains adults ready to fly, *i.e.* royal forms that have not yet paired, the formation of royal substitutes takes place nevertheless, as described above. In other words, the winged sexual forms if present do not become kings and queens, when these are needed in the nest, but substitute forms are made. Only after the nuptial flight do the royal forms become the heads of new colonies.

The food of Calotermes consists of wood, matter excreted or disgorged by other individuals, the exuviæ, the corpses of

other individuals, their own saliva and that of others, and water. The fæces form an important element in the diet. "When a calotermite wishes to feed, he accosts one of his fellows and caresses the abdomen with the antennæ and palpi. If the one thus accosted is prepared to eliminate, he at once extrudes the scybalum from the anal aperture. The other then removes it, chiefly by aid of the auxiliary palpi, and usually in two operations separated by a short interval, drawing it at first half, and then completely out. He then rapidly seizes it with the mandibles, suspending his caresses for this purpose, and when he has possessed himself of it nibbles at and ingests it little by little." [1] Pellets can sometimes be seen in the mouth composed of regurgitated food, which is at times used for building, but may be seized and eaten by another individual. The saliva may be used either as cement in building or as food for others. It is given in abundance to larvæ that are too young to eat wood, and to those that are in course of becoming royal substitutes. These individuals, fed with saliva, "exhibit a great transparency of the abdomen, an indication that they are in process of becoming royal substitutes." Their digestive tract contains no protozoans that are usually present in other forms. Possibly they have been killed by the saliva. These and other facts suggest that the saliva is the cause of the transformation of young termites into substitute forms. What determines whether a young termite is to become a soldier or a worker is not known; but Grassi thinks that this difference is also determined by the food.

These experiments and observations leave little doubt that the different castes of termites arise from the same kind of egg, and are not predetermined in the egg. Each egg has the possibility of becoming a royal form, a royal substitute, a worker, or a soldier. It is probable that the results depend on the amount or the kind of nutrition that is given to the young by the older members of the community.

In the honey bee the relation between the food and the development of the worker and queen is better understood. It appears

[1] Translated by W. F. Blandford.

that any fertilized egg may produce a fertile queen, and the amount of food supplied to the young larvæ determines the result. If the old queen dies and young larvæ are present that are not more than a day or two old, the workers can produce one or more new queens by feeding the young grubs on the royal jelly.

Leuckart found that the food of the young larvæ of queens and workers is the same for the first three days and then is changed for the worker while the queen grub continues to be fed with the same food rich in honey. At this time the female genital organs appear, so that if the weaning of the worker grub does not take place promptly, any excess of the royal jelly may cause the ovaries to continue their development and produce a fertile worker.

In the bees all the workers are females with undeveloped sexual organs. They have all the marks of perfect insects in other respects, and cannot, therefore, be said to be neotenic.[1] The males or drones develop from unfertilized eggs, and their characters are not affected by the kind of food they receive, except that a drone fed on royal food may become unusually large.

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[1] In this case it is the germ-cells that fail to develop, while the body tissues pass over into the adult condition. In a sense this is the converse of neotenia.

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CHAPTER XX

ALTERNATION OF SEXUAL AND PARTHENOGENETIC FORMS

PARTHENOGENESIS plays a double rôle in the animal kingdom; in some species parthenogenetic generations alternate with sexual ones, and in such cases both the male and the female individuals develop from unfertilized eggs; in other species, where no such alternation of generations exists, the fertilized eggs produce individuals of one sex, the female as a rule, and the unfertilized eggs produce the other sex. It may be well to keep these two categories apart, although intermediate conditions are not unknown, as where unfertilized eggs produce both males and females. The cases in which external conditions influence the kind of reproduction belong, for the most part, to the first category, where parthenogenetic and sexual generations alternate.

Alternation of Generations in the Aphids and Phylloxerans

It was pointed out in the last chapter that in the group of Aphids an alternation of parthenogenetic and sexual generations occurs. In some species the change from the one to the other method depends on a change in external conditions; but in other species a definite succession of generations exists, and the change is less obviously connected with the effects of the environment.

The discovery that many of the aphids give rise during the summer to young without the presence of males appears to have been first made known by Leeunwenhoek in 1695, and later by Réaumur in 1737, but the series of experiments carried out by Bonnet in 1745 attracted more widespread interest in this mode of development, because of his philosophical discussion of the phenomenon.

The first experiment showing that external influences have an effect on the mode of reproduction was that of Dageer in 1773, who kept plants containing aphids in a warm place, and found that the sexual forms did not appear. The cycle of the species with which he worked was shown, therefore, to be an open one, its completion depending on external conditions. Kyber in 1815 raised fifty successive generations of parthenogenetic individuals during four years by keeping the animals and their food plants in the warmth during the winter. It would be interesting to know whether, in warm climates where the plants — the rose, for instance — grow throughout the year, the sexual form ever appears.

The earlier students of parthenogenetic development of the aphids were much puzzled over the viviparous production of young in the absence of males, and it was thought by some observers that the development could not be by means of eggs, but was the result of a process of internal budding. It was shown later, however, that the embryo arises from an egg produced in an ovary. The ovary and the way in which the egg appears in it are nearly the same as in other related species in which eggs are deposited; but a remarkable condition exists in the viviparous aphids: the egg begins to develop almost immediately after it has left the ovary, when it is very small and when from comparison with other species it appears to be in a very immature condition. However, since the ripening process of the nucleus is the same as in other parthenogenetic eggs that are larger, and are regularly deposited,[1] there is little real basis for calling the aphid egg immature, because it is small when it begins to develop. The commoner forms of aphids, the rose aphid, for example, pass through the following series of forms, with some variations. In the spring, the eggs (that had been deposited on the stems of the food plant) complete their development, and parthenogenetic wingless females emerge. These grow rapidly to the full size, and produce a new generation of wingless forms amongst which a few winged individuals often occur. This

[1] The phylloxerans, for example.

process continues throughout the summer, but even during this time, especially if the food plant becomes crowded, winged individuals appear, and these are also parthenogenetic. They usually fly away when the sunlight falls on them, and if they are fortunate enough to find a new plant of the right kind they start there a new generation of parthenogenetic forms. In the autumn the males and females appear. The males are winged, the females are wingless. The parents of the males are also wingless, but the parents of the sexual females are winged, these conditions varying, however, in different species of aphids. In some both the males and sexual females are winged. Moreover, according to Lichtenstein, while it is usual for the mother of the sexual forms to produce only males or only females, in certain species both sexes are produced by the same parent. The males and females pair, and the sexual eggs are deposited on the food plant, where they remain over winter. In the spring only parthenogenetic females hatch from these eggs. Even if kept in a warm place, the winter eggs will not develop until several months have passed.

In cases like this one of the rose aphid, the whole cycle completes itself on the same plant. The rose aphid will also, under compulsion, live on other plants and even multiply there with great rapidity, as on the dock, for example. I have tried in a few cases to produce the sexual forms by changing the food plant, but so far without success.

Balbiani has discovered the important fact that the same female may give birth to parthenogenetic individuals, as well as to sexual females and males. This result removes all grounds for the assumption that there are two lines of parthenogenetic individuals, — one culminating with males, the other with sexual females. Balbiani isolated the females of Centaurea jacea at the time of year when the transition from the parthenogenetic to the sexual mode of reproduction was taking place. Each day the number and the kind of young produced was noted. The number varied from one to seven per diem. After a day of great productiveness there followed one or more days when no young

or very few were produced. Some females gave birth only to parthenogenetic young, others first to parthenogenetic and afterward to a mixture of parthenogenetic and sexual young. The following records give the kind and the number of offspring for ten isolated females.

The parthenogenetic females are indicated by P, the males by M, and the sexual females by F.

First female, Aug. 21 to Sept 5.
3P, 3P, 2P, 4P, 5P, 3P, 4P, 6P, 3P, 3P, 2P, 3P, 3P, 1P, 1P. Total, 46 P.

Second female, Aug. 21 to 25.
{3P / 2F}, 3P, {3P / 3M}, 2P, 3P. Total, 14P, 3M, and 2F.

Third female, Aug. 23 to 28.
2F, 2F, 3F, 6F, 3F, 2F, 1F. Total, 19F.

Fourth female, Aug. 26 to Sept. 20.
6P, 5P, 5P, 4P, 3F, 2F, o, {1M / 1F}, {2M / 3F}, 2M, 4F, {1M / 1F}, 5F, 3F, 4F, 9F, o, o, o, 2F, 1F, 1F, 2F, o, o, o. Total, 20P, 6M, 44F.

Fifth female, Aug. 3 to Sept. 19.
4F, {5M / 4F}, {1M / 1F}, 1M, {2M / 3F}, {1M / 3F}, {1M / 3F}, 3F, 6F, 3F, 1F, 4F, 2F, 1F, 7F, 1F, 6F, 4F. Total, 11M, 56F.

Sixth female, Aug. 31 to Sept. 20.
{2M / 2F}, 5F, {4M / 1F}, {2M / 2F}, {3M / 1F}, {3M / 6F}, 3F, 7F, 2F, 4F, 5F, 3F, 6F, 1F, 2F, 1F, 5F, o, o, 1F, 1F, o, o. Total, 14M, 56F.

Seventh female, Sept. 16 to Oct. 1.
3F, o, 2F, {1M / 1F}, {4M / 1F}, {2M / 3F}, 5F, 4F, 4F, 5F, 2F, 4F, 2F, 4F, 5F. Total, 9M, 51F.

Eighth female, Sept. 16 to Oct. 7.
{1M / 1F}, 3F, 1M, {2M / 4F}, 2F, 4M, {1M / 1F}, {1M / 1F}, {2M / 4F}, 1F, 2F, 2F, 3F, 3F, o, 3F, 2F, 1F, 4F, o, 2F, 2F, o, 1F, 3F, o, 2F, 1F, 2F, o, 1F, 1F. Total, 12M, 55F.

Ninth female, Sept. 16 to Sept. 26.
4F, 1M, 1F, {3M / 1F}, 1M, o, 3F, o, 4F, 4F, 1F. Total, 5M, 18F.

Tenth female, Sept. 16 to Oct. 4.
3M, {1M / 2F}, {2M / 2F}, 1F, 4F, 3F, 3F, 1F, 3F, 4F, 1F, 1F, 2F, 2F, 1F, o, o, 1F, 1F. Total, 6M, 32F.

The results are summed up as follows: Toward the end of the season an individual may first give birth for a few days to a mixture of parthenogenetic and sexual individuals, but at this time the males predominate as a rule. The parthenogenetic young now cease to appear, and only sexual individuals are born. After two or three days of mixed sexual broods, the males cease to appear, and there then follows a long series of sexual females, that terminates only with the death of the mother. Not more than 20 per cent of the sexual forms were males in one of the species studied by Balbiani, and many of these died in the larval stages. Certain females begin at once to produce sexual forms without having first produced parthenogenetic young.

Balbiani isolated young females about to give birth to sexual young, and placed them on young branches of the same plant in order to see whether the kind of young produced is affected by the condition of the food plant. They continued, despite the change, to produce sexual individuals throughout the rest of their lives. Conversely, a female producing parthenogenetic young was placed on a branch cut from the plant. She continued to produce parthenogenetic young. As the branch became dry she acquired wings and flew away. Balbiani concludes that food does not produce any effect on the mode of reproduction unless the organism is "predisposed to submit to its influence." This predisposition appears at certain times of year characteristic for each species. Possibly the results may be interpreted, I think, to mean that external conditions require more than one generation to produce their effects, and when once effected the mode of reproduction for that individual cannot be altered. It remains to be shown, I think, that there is an inborn predisposition that is independent of external conditions to produce sexual forms. On the contrary, the possibility of prolonging the parthenogenetic series indefinitely by proper conditions shows that the predisposition is connected with external changes.

Stevens has recently confirmed Balbiani's discovery that the

same female may produce both parthenogenetic and sexual young, or males and females, or only one sex alone.

In contrast to species like the aphids with an open cycle, there are other species with closed cycles, and in some of these there is an alternation of plants closely associated with an alternation in the successive forms; but it is important to note that the change in the aphid has already been initiated on the old plant before the migration to the new one takes place. This is also true in some cases for the sexual forms. Some examples will make my meaning clearer.

There are two American species of aphid that alternate between the red birch and witch-hazel, producing galls on the latter and crinkling of the leaves of the former. Pergande has made out the following life-cycle for these species: One species, Hormaphis hamamelidis, passes through seven generations in its life-cycle, and the forms that appear in this cycle show great differences in structure. The eggs that have wintered over on the witch-hazel hatch about a week before the young leaves appear, and the young animals congregate on the still-closed buds. They settle finally on the under side of the unfolding leaves, and insert their bristles in the substance of the leaf. Within a few days the gall begins to develop, a swelling appearing above and a cuplike depression beneath. The gall develops rapidly and assumes the form shown in Fig. 23, 1 a, 1 b. The stem-mother, as this first inhabitant of the gall is called, moults three times before assuming the full size (Fig. 2). She gives birth to many young, which cover the inner walls of the gall; they moult four times and become winged (Fig. 3). These migrants gradually leave the galls during June. Each contains about 50 embryos. They fly to the birches, and deposit their young on the under sides of the leaves. These young form the third generation. They also moult four times and produce the aleurodiform stage (Fig. 4). Each is flat and surrounded by a circle of waxy rods, and gives birth to young of the fourth generation that are like their parents. The fourth generation produces a fifth similar to the two last. A curious fact regarding these

FIG. 23. Hormaphs hamamelistes, showing life-cycle of non-sexual, winged and wingless sexual, wingless forms. (After Pergande.)

aleurodiform stages is that many of the females are devoid of eggs and die after reaching maturity, others give birth to only a few young, while the most prolific produce only about 10 to 15 young.

The individuals of the fifth generation give birth to young while still on the birch, which become the return migrants (Fig. 5). They reach the adult condition toward the end of August. These return migrants are like the earlier migrants, except that they are smaller. They fly to the leaves of the witch-hazel, and give birth there to the sexual forms, male (Fig. 7) and female (Fig. 6). Pairing occurs, and 5 to 10 winter eggs are laid by each female around the bases of the leaf buds. From these eggs the young hatch in the spring.

The other aphid, Hamamelistes spinosus, described by Pergande, also alternates between the witch-hazel and the birch, producing on the former large spiny galls (Fig. 24, 1), and on the birch a peculiar crinkling or gall-like formation of the leaves (Fig. 5). The winter egg is laid in June or July, but does not hatch until the spring of the following year. Two years are required to complete the life-cycle. The young that emerge from the egg on the witch-hazel find a young flower bud, and settling on it begin to suck its juices. The bud becomes a gall inclosing the insect. Each gall has an opening at the bottom (Fig. 1). The stem-mother when full grown is shown in Fig. 2. She gives birth to a large number of young, possibly 300 in all, and the young fill the gall. These young become, early in July, the migrants (Fig. 3). Each contains 30 to 40 young. The migrants alight on the birch leaves where the young are deposited. The young feed on the leaves, then move to the twigs, and settle down close to a bud. After three moults they become degenerate, scale-like insects — they are the coccidiform or hibernating females (Fig. 4). In the following spring they give birth to young that migrate to the new leaves, where they settle down between the folds. Their presence causes the edges of the leaves to turn under while the upper surface of the leaves bulges out into ridges and corrugations (Fig. 5). In about

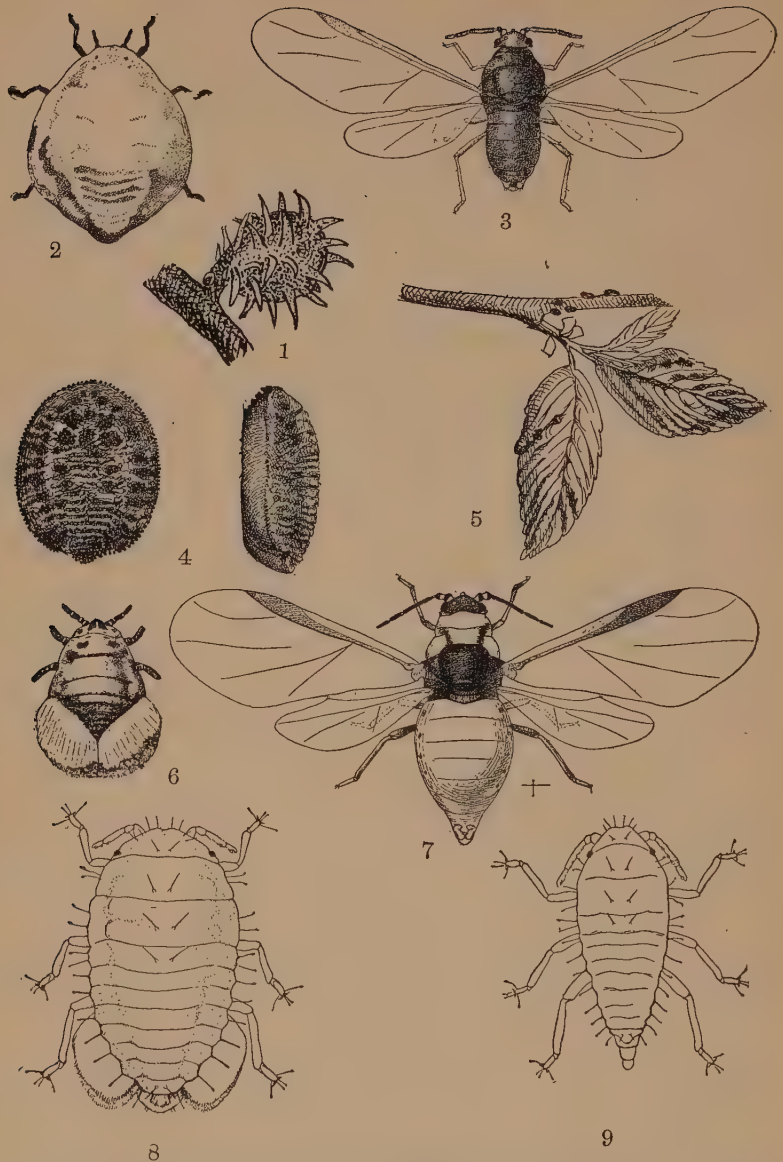

FIG. 24. Hamamelistes spinosus, showing life-cycle of non-sexual, winged and wingless; and sexual, wingless forms. (After Pergande.)

20 days they become mature and produce numerous young of the fourth generation (Fig. 6). These produce in turn the fifth generation, that is, the winged migrant (Fig. 7). Some of the individuals of the fifth generation do not become winged — possibly these short-circuit the life-cycle. In June the migrants are ready to leave the birch and migrate to the witch-hazel, where they give birth to the sexual males (Fig. 9) and females (Fig. 8). They pair and the females deposit one to five large eggs on the twigs near the flower buds. These eggs remain undeveloped through the whole summer and the next winter, and hatch only in the following spring, when they move to the young flower buds and produce there the gall of the witch-hazel.

A number of other aphids also alternate between two plants, although the entire life history is not so well known as in the last cases. In the aphid of the apple tree, Aphis mali, several apterous generations occur in the spring. Winged forms then appear that have been supposed to migrate to the stems of wheat or grass, and there produce, parthenogenetically, wingless forms. In time, winged individuals again appear which migrate to the apple tree, producing the sexual forms that unite and produce the winter eggs from which the new generation appears in the following year.

The aphid of the elm, Tetraneura ulmi, of Europe has, according to Blochmann, the following life-cycle: The winter eggs hatch about the end of April. The aphids produce galls on the leaves within which viviparous young are born. These are winged and leave the galls. They disappear for a month, and were supposed to live on some other plant, but according to Riley for an American species they live on the bark of the elm tree, where they produce one or more generations. Winged forms appear in August, returning to the branches, where they deposit their eggs, from which sexual males and females appear. These pair, and one fertilized egg is laid by each female on the bark of the tree, where it remains over winter and produces in April the first generation of summer forms.

The species of the genus Chermes have a very complicated life

history, as shown by Blochmann, Dreyfus, and others. The young appear in the spring on the fir. They become mature and deposit eggs. The young developing from these eggs produce galls, within which they mature as winged individuals. Most of these leave the fir and go to the larch, where each female deposits about 40 eggs, which, hatching in 10 to 14 days, produce young that feed on the leaves. Later these wander to the stem, where they hide in the crevices throughout the winter. In the spring they grow larger and begin to lay eggs about the middle of April. The eggs soon hatch and the young wander upward to the young needles, on which they feed and grow to winged parthenogenetic females. These leave the larch about the end of May and fly to the fir, settling down on the under sides of the old leaves, where they deposit 8 to 10 stalked eggs from which sexual males and females develop. These pair and the female lays one egg on the stem. The eggs develop slowly, the young emerging in October. They wander to the bases of the buds, stick the proboscis into them, and winter in this condition. In the spring the female deposits many eggs, from which the young that emerge are those that produce the galls first mentioned. This brings the cycle back to the starting point.

There is also in Chermes what is known as a parallel or collateral series. Part of the parthenogenetic females on the fir that are late in leaving the galls remain on the fir, and deposit their eggs there (instead of on the larch). The young wander to the ends of the branches, where they remain until the next spring with the proboscis stuck into the tissues of the buds. In the spring they produce galls. Presumably the cycle may begin again from the individuals that emerge from these galls, which have, as it were, short-circuited the life-cycle.

It is of great interest to observe that the sexual forms do not appear in this short-circuited generation that remains on the fir, and the inference is plausible that the conditions existing on the larch are those that call forth the sexual forms.

In another species, the phylloxera of the grape, the alternation of generations takes place between the roots and the leaves.

Wingless parthenogenetic individuals are found during the winter on the roots, where they cause swellings, or gall-like thickenings. Immense damage has been done to the vineyards of Europe by these root-inhibiting forms. At the end of June, winged parthenogenetic individuals develop, and wander upward to the leaves. They deposit eggs of two kinds, — large ones that produce the sexual females, and smaller ones that produce the males. The males and females pair, and the female deposits on the bark a single large winter egg. In the spring this egg produces a wingless female that goes to the leaves and produces there gall-like growths. Offspring are produced, some or all of which find their way in time to the roots, where they remain over winter.

In the phylloxerans of the hickories the life history is somewhat the same. Following Pergande the cycle for most of the American species is as follows: From the winter egg a female — the stem-mother — is produced. She wanders to the young leaves and fixes her proboscis in the under surface. A gall develops around her, within which she lays eggs that give rise to winged migrants. These leave the gall by the opening on its under surface, and fly away. Those that alight on the bark of the hickory deposit their eggs in its crevices. These eggs are large or small, and produce respectively female or male individuals. These pair, and the female lays a single large egg that overwinters and gives rise in the following spring to the stem-mother. In a few species the stem-mother produces forms that are, as a rule, without wings. These deposit the large and small eggs within the gall. Presumably the sexual forms that hatch from these eggs leave the galls and deposit the fertilized egg on the stem.

The life histories of these different forms offer many points for consideration, and what is more important would seem to give unusual opportunities to test the factors that lead to the transformations of one form into another. What would happen, for example, if the life-cycle were to be artificially altered at different points in its course by transferring the individuals prema-

turely to other plants or by preventing the normal migration? A few attempts that I have made in this direction show that the experiment is not always easily carried out, at least in the forms that I have used, since if transferred too soon to the alternative plant host the individual often dies. It would no doubt be easier to obtain results by preventing the normal migration. In the case of the fir, where migration is sometimes deferred naturally, at least for a percentage of the individuals, the cycle goes back to its starting point. What nature has done in this instance we should be able to imitate in other species by inclosing in gauze bags on their plants the individuals about to migrate.

It is important to note that the different parthenogenetic individuals of the same species that occur on the two plants may differ enormously in structure in some cases, as shown especially in the case on Hormaphis hamamelidis. The change must be effected not by the new plant but by the original one; for the parthenogenetic young may be fully developed before the migration takes place, but whether their subsequent changes on the new plant, that are sometimes very great, are brought about by the new plant remains to be shown experimentally.

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CHAPTER XXI

INFLUENCE OF EXTERNAL CONDITIONS ON THE LIFE-CYCLE OF THE LOWER CRUSTACEANS

In the lower subdivisions of the group of Crustacea there are a number of forms in which parthenogenetic and sexual modes of reproduction alternate with each other. Experiments have shown in some cases, at least, that the occurrence of these two modes of reproduction is dependent on external conditions. Here, again, we meet with the same fact, referred to in the case of the aphids, that the external conditions determine, in the main, whether the reproduction is to be parthenogenetic or sexual, not whether individuals of one or the other sex appear. In other words, the effect is not to produce males or females, but a different mode of reproduction, involving only females in the case of parthenogenetic, and both males and females in the case of sexual forms. It might be claimed that the change only brings about the appearance of males when the sexual generation appears, while females develop under both conditions. This view of the matter does not seem to hold in those cases where the sexual females are quite different forms from the parthenogenetic females, as in the aphids, but in the case of the crustaceans to be described this claim might be maintained. It is also true that the proportion of sexual females and males may be to some extent affected by the character of the external conditions, but this may be a different side of the question, and will be discussed later.

Artemia salina reproduces both by summer eggs that develop in the embryo sac, the young being born alive (viviparous) or by means of resting eggs that are deposited (oviparous); but the time of year at which the one or the other method is followed

seems to differ in different localities. In some local varieties of this species the males are always present and abundant (as in England, Odessa, Utah, and Cagliari), while in other races the males are rare and not more than one or two males to a thousand females are found. In the latter case all the summer eggs develop by parthenogenesis. Whether the winter eggs must be fertilized in these forms is not known. In the other cases both the summer and the winter eggs are fertilized, and fail to develop if they are not, — at least this has been definitely shown to be the case at Cagliari by Artom.

Most of the daphnias, or water fleas, show an alternation of parthenogenetic and sexual forms. Many of the more familiar species pass through the following cycle. From the winter egg there emerges in the spring a female parthenogenetic individual. Her offspring are also parthenogenetic, and throughout the summer a series of these forms succeed one another in rapid succession. In the autumn, males and sexual females appear, and the latter, after fertilization, produce the winter eggs from which the new brood of the following year emerges.

This cycle differs somewhat in different species, and it is known that sometimes males and sexual females are found during the summer, and that in other species they appear under special conditions. Kurz made some experiments which he thought showed that the sexual forms appear when the water becomes stale or begins to dry up. By hanging pieces of raw cotton over the edges of the jar in which the daphnias lived, the water was slowly drawn off, and after 14 days it was reduced to about one sixth of its original volume. The experiment was carried out in May, and many males and sexual females appeared in the four different species present. In another experiment he failed to obtain the same result, although in foul water the sexual forms appeared.

Weismann has made a most elaborate study of the life history of the Daphnidæ. He believed that his observations and experiments show that external factors do not determine the appearance of the sexual generation, but that the change is due

solely to an internal factor. The latter, he believes, is the outcome of natural selection which has acted in such a way that the internal mechanism has been adjusted to meet the changes in the environment, without, however, being affected directly by them. In other words, natural selection has changed the life-cycle so that it undergoes a parallel series of changes to the cyclical changes in the environment, or as Weismann has put it, "The organism is so constituted that it reproduces sexually at the proper time, and it is to a certain degree a matter of no consequence what external conditions exist at that time, so long as they are not of a sort to very materially interfere with the process of assimilation or to threaten the life of the individual." In other words, natural selection has wound up the individual to go in the same time as the environment.

Weismann points out that the usual appearance of the sexual forms in the autumn has suggested that the cold brings about the result, but this is disproven by the fact that in the early spring the water may be as cold as in the autumn, yet in the spring the reproduction is only by parthenogenesis. He made an experiment that confirmed this conclusion. During the summer he kept pieces of ice in an aquarium in which a large number of individuals lived, so that the temperature was reduced to from 5° to 10° C. The daphnias continued to reproduce parthenogenetically, although more slowly.

In another way, Weismann thinks, the insufficiency of the temperate hypothesis is shown. Daphnias that live in swamps (Polyphemus, for example) have a double sexual period: the first at the beginning of July, when the water is at its warmest; and the second at the end of October, or the beginning of November, when the temperature is near the winter minimum.

Weismann does not think that the condition of the food supply can account for the result, because he believes that food is always abundant. Most species of daphnias live on fine slime or particles of organic matter, sticking to the bottom or suspended in the water. Weismann thinks there is a superfluity of this material at all times. He states, moreover, that the sexual genera-

tion appears when food must be at its time of greatest abundance. That Weismann is probably mistaken in this regard will be shown presently.

Weismann also rejects Kurz's idea that the drying up of the water causes the sexual forms to appear, and bases his objection most justly on the failure on Kurz's part to carry out control experiments in which the water was not diminished. Weismann points out that the sexual forms often appear in confinement when the level of the water remains the same. Schmankewitsch's suggestion, that increasing the amount of salt contained in the water causes the parthenogenetic forms to give rise to the sexual generation, is also rejected by Weismann. Schmankewitsch pointed out that Moina rectirostris lives in small pools in the spring and autumn; it disappears in the summer when the salt becomes too strong, but before this occurs the sexual generation appears. Weismann objects that while the facts may be correct it does not follow that the salt is the cause of the change; for in other localities the same species of Moina lives in fresh water and at all times of the year, and in every generation except the first (that hatches from the winter eggs), brings forth males and sexual females.

Weismann carried out some experiments which show, he thinks, that external conditions do not regulate the alternation of generations. He found when two lots of daphnias are kept in separate dishes under conditions as similar as possible that one set may produce males and sexual females, while the other set continues to reproduce parthenogenetically. It seems to me hazardous to claim that the conditions are the same in any two such dishes, for while light, temperature, and the amount of water may be the same in both, the food supply may be very different, depending in large part on the number and kind of animals that are devouring the food. Experience will show that it is well-nigh impossible to keep the relation between the plants (that serve as food), the bacteria, and the animals in a constant relation in any two dishes. Any initial difference at the beginning (and such must nearly always exist) may lead to very different

results. Weismann cites the following experiments in support of his statement. Six young daphnias, born parthenogenetically from the same mother, were isolated each in a separate glass. Fourteen days later No. 1 had produced three parthenogenetic young; No. 2, eight of the same; No. 3, six; No. 4, five; No. 5, seven sexual females and three males; No. 6, five parthenogenetic females.

In another experiment a male and a female were placed in the same small glass on March 5. They belonged to the fourth generation from the winter egg. They were not observed to pair. Three weeks later 8 parthenogenetic females were present. After another 3 weeks 50 young were counted, of which many were males. Ten days later there were 18 sexual females and 5 males. A week later numerous young were found, and 9 days later still, when they were counted, there were found 3 females with winter eggs, 20 parthenogenetic females, 1 male, and 79 young. In this experiment the sexual forms did not appear for some time; but in a parallel experiment beginning with 25 males and 8 females (March 24) the sexual forms appeared at once. It is difficult to understand why Weismann should conclude from these experiments that the life-cycle is independent of the environment. It is more probable that there was present some unknown condition that caused the difference in the results. One such condition may have been the crowding with the consequent decrease in the available food.

Weismann has laid a good deal of emphasis on the differences in the life history of species of Daphnidæ that live under different conditions. Thus monocyclic species in which the sexual generation appears only once in the course of the year are found in large bodies of water that never dry up, — in lakes, ponds, swamps, and in the ocean. Sida crystallina is a species of this kind. Throughout the summer only parthenogenetic individuals appear, and in the autumn males and sexual females. Polycyclic species inhabit puddles and small swamps that are often dried up. The winter eggs can withstand the drying, but not the parthenogenetic adults; therefore in order to exist in

such localities the winter eggs, more appropriately called the resting eggs, must be often produced. Such, in fact, is the case, and males and females may appear more than once a year. For example, Moina rectirostris and M. paradoxa usually produce three to five successive parthenogenetic broods, but amongst these, sexual forms are always to be found, even at times in the first parthenogenetic generation, but always in the second and third. Again in Daphnia pulex, which lives in swamps, the first generation consists of parthenogenetic individuals. Males and females may appear in the second; they are not infrequent in the third, and almost always present in the fourth, fifth, and sixth generations.

There are a few species that seem to be acyclic, *i.e.* produce no sexual forms at all, but throughout the winter and the summer reproduce by parthenogenesis. Weismann believes that this is a local condition, and that in other localities the same species may have a sexual generation. Chydorus sphærius produces in Freiburg only parthenogenetic females, but in other places sexual forms have been found.

From the conditions under which these forms live Weismann thinks that through natural selection the life-cycle has been made what we find it to-day, so that each species has become adapted to the special conditions under which it is found. It may be pointed out that the results can just as readily be explained by assuming that, the life-cycle being what we find it, certain species can live only in certain localities and others in other localities. How the species having these cycles originated, is a question that we need not discuss at present.

There are certain facts connected with the reproduction of these crustaceans that are of general biological interest. The same individual may alternately produce winter and parthenogenetic eggs. If, for example, the winter egg is not fertilized, it goes to pieces, and this "acts as a stimulus" to further parthenogenetic reproduction. Four cells go to produce a parthenogenetic egg, three of them serving as food for the fourth, but a large number of cells contribute to the formation of the winter

egg. It is interesting to note that if the winter egg is not fertilized it does not develop parthenogenetically, although it is better supplied with food than the parthenogenetic egg. Thus while there is a sharp distinction between the two kinds of eggs, there is no such distinction between the females that produce them; for the same female may first produce one sort and then the other. If external conditions determine which kind of reproduction is to take place, they do so by affecting the kind of egg rather than the kind of individual; but it is interesting, even here, to notice that the conditions that call forth the males are those that call forth the production of the winter eggs in the females.

The winter egg is also a resting egg, *i.e.* although after fertilization it passes through the cleavage stages its further development is there arrested, even if placed in water at a favorable temperature. In some species it has been found that the resting eggs will not develop further unless they are first dried[1] — an excellent adaptation for preserving the race, for the eggs remain undeveloped until the pool becomes dry, and later may stock the pool again with a new brood. In other species, in Moina and in Daphnia, according to Weismann, the resting eggs will develop after a time if kept continuously in water. The resting eggs of Moina paradoxa took from 30 to 40 days to develop in June, but in September only 10 days. For Daphnia pulex, the egg took from 18 to 31 days in the spring, and from 47 to 60, or even to 80, days in September.

A series of experiments have been recently carried out by Issakowitsch, under the direction of R. Hertwig, that go far toward showing that external conditions regulate the life-cycle of the daphnias.

Issakowitsch kept a species of Daphnidæ, Simocephalus vetulus, at different temperatures and obtained different kinds of individuals according to the temperature employed. For instance: a parthenogenetic female was isolated and kept at 24° C. Between February 6 and April 5, 6 generations appeared

[1] Brauer found that the eggs of Apus will not develop unless first dried, and Spangenberg found that this is also true for Branchipus.

composed of 70 broods. There were about 500 individuals produced. All were parthenogenetic, and no males and no sexual females appeared. In another similar series a few males and sexual females developed, but the tendency seemed to be to produce purely parthenogenetic forms. When kept at room temperature, 16° C., an isolated parthenogenetic female produced from February 6 to April 15 two generations, and 13 broods in all, composed of about 100 individuals. The first brood consisted of females and 5 males. The sixth brood was composed of parthenogenetic females which brought forth males, etc. Another culture under the same conditions gave 30 broods of 250 individuals, Again there was observed a transition from females to males through an intermediate mixed brood. In both cultures the females of the first generation produced the shell for the winter egg — the so-called ephippium. This was then thrown off because the egg was not fertilized. The next brood of the same individuals consisted only of parthenogenetic females, but the next brood after this was made up either entirely of males or else another ephippium was formed. When a female produces the ephippium with the winter egg in it, the sexual condition is present, and therefore it will be observed that the same individual may function at one time as a parthenogenetic and at another time as a sexual female. In the case last mentioned where another ephippium is produced this may be thrown off and the following brood will be again males or another ephippium develops. When kept in the cold, 6° C., there is a still stronger tendency to produce sexual forms. This is shown in the two following experiments. All the offspring of one female were taken from the warm culture and separated into two groups. One set was kept at 24° and the other at 8°. The results for the two cases are shown below:—

24°	8°	24°	8°
♀	♀	♀	winter egg
♀	♂	♀	winter egg
♀	winter egg	♀	died
died	winter egg	died	

At the higher temperature three successive parthenogenetic female broods appeared. In the cold the females brought forth, in the one case, first parthenogenetic forms, then males twice, and then winter eggs twice. In the other case (the right-hand table) the offspring of five sisters kept in the cold produced winter eggs twice and then died. These results show that at high temperatures only or largely parthenogenetic females appear, while at a lower temperature the sexual method of reproduction for the females and the appearance of males occurs.

Issakowitsch attempted to determine whether temperature acts directly or only indirectly by affecting the condition of nourishment. Females containing eggs in the brood pouch were selected in order to be certain that from the beginning of development the young themselves were subjected to a condition in which food was insufficient. These animals were put into pure filtered spring water and left there for eight days. This brood after hatching produced always sexual animals, males, and females bearing winter eggs. The results show that even at the high temperature the sexual part of the cycle appears if food is lacking. Issakowitsch concludes, therefore, that the animals kept in the cold produce sexual forms, not because of the cold, but on account of the influence of the cold on certain conditions of nourishment in the ovary, and he points out the following facts that seem to support his point of view. In the first place, even in the cold if an ephippium is first produced and then thrown off (fertilization not having occurred) the next brood consists of parthenogenetic females, whatsoever the other external conditions may be. Issakowitsch offers the following interpretation of the change. If the winter egg in the ephippium is not fertilized, it is absorbed, and furnishes the ovary with food materials. Owing to this better condition of nourishment the next generation is parthenogenetic. After this brood has been set free the equilibrium between temperature and food is again established, and external conditions will determine what the subsequent events will be.

There are certain peculiarities in regard to the origin and

development of the parthenogenetic and the "winter" egg that have a bearing on the present question. The wall of the ovary swells up, and its cells become filled with a fluid when the parthenogenetic egg is about to develop. The egg seems to get its nourishment from these cells. On the other hand, when the winter egg develops the walls of the ovary do not enlarge, but the egg develops at the expense of the surrounding cells that afford the nourishment for its growth. The conditions in the ovary itself would seem, therefore, to be determinative as to which kind of egg will develop. It should be observed, however, that we do not know whether it is the same cell that becomes in one case a winter egg and in the other a parthenogenetic egg. In fact, Weismann has stated that the two kinds of eggs come from different parts of the ovary. The special conditions that lead to formation of the male egg are unknown.

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CHAPTER XXII

INFLUENCE OF EXTERNAL CONDITIONS ON THE LIFE-CYCLE OF THE ROTIFER; HYDATINA SENTA

In the rotifer Hydatina senta, both parthenogenetic and sexual reproduction takes place, and appears to be directly determined in part by external conditions; but also in part by an internal factor, viz. by the early fertilization of certain females. Maupas and later Nussbaum have carried out experiments with this form, and while they agree on certain essential points, especially in regard to the mode of reproduction depending on an external factor, yet Maupas believes the effect is produced by the temperature, while Nussbaum thinks that the cause of the result is the food supply, which may be affected by the temperature in the sense that at a higher temperature more food is required than at a lower, because the life processes go on faster.

The males of Hydatina senta are smaller than the females, measuring .25 millimeter and the females .75 millimeter. The males take no food, and have, in fact, no digestive tract. They are not sexually mature when they leave the egg capsule, but the sperm ripens during the first day. They live two or three days only, but may fertilize several females during that time. The females require a great deal of food and will die in two days if starved. In five minutes a hungry female will fill her digestive tract, and begin to empty it in 20 minutes. Microscopic organisms are eaten, Euglena being the chief food.

The females may produce the soft-shelled summer eggs or the hard-shelled winter (or resting) eggs. The summer eggs develop without fertilization, and may produce either males or females, one sex or the other being produced by an individual, not both by the same individual. The winter eggs are fertilized;

in fact, they do not appear at all unless previous union with a male has occurred.

Maupas found that of 796 females isolated from males only parthenogenetic eggs were produced (male or female). Of 172 females to which males had been added at the right time (about 6 hours after hatching), 84 produced winter eggs and 88 parthenogenetic eggs (male or female). In another experiment 822 females were used, and 342 of these were observed to unite with males. Of these (342) there were 252 that laid winter eggs, the other 90 produced summer eggs. The ratio of individuals laying winter eggs to those laying summer eggs is, therefore, 74 to 26. The remainder of the 822 females that were not seen to pair, 480 in number, gave the following results: 361 produced males and 119 produced females. The ratio is 75 to 25. This is nearly the same ratio as the ratio of winter eggs to summer eggs given above. From this similarity in proportion Maupas concludes that only male eggs can be fertilized, and these become winter eggs. The winter eggs give rise solely to females. If this conclusion is established, it follows that fertilization changes the sex of the egg, as in the bee. Nussbaum believes the similarity in the ratios may be purely accidental, but will not deny that the conclusion may be correct.

Maupas tried to show that temperature is the factor that determines the fate of the eggs. If the temperature is lowered, females are produced. If the temperature is raised, males are produced. He gives the following experiment to establish this conclusion. Five *immature* females were kept at a temperature of 26° to 28° C. They laid 104 eggs, of which 97 per cent produced individuals that laid male eggs and only 3 per cent produced individuals that laid female eggs.

In the control experiment five immature individuals from the same culture were kept at a temperature of 14° to 16° C. They laid 260 eggs, of which 5 per cent became male and 95 per cent became female producers. It will be noticed that in these two experiments both the mother and the eggs she produced were under the same conditions of temperature, hence the effect

may be produced either on the eggs in the ovary or on the eggs after they are laid, or on the embryo itself. Another experiment described below is required to settle this question. The main point at present is that the sex changes with the temperature.

Nussbaum has objected to this conclusion on the grounds that it is not clear whether Maupas's calculations rest only on the relative sizes of the eggs produced, or on the kind of individuals that emerged. If on the former, the result must be inconclusive because many eggs of intermediate size are usually present that cannot be accurately referred to one rather than to the other sex. It is improbable, I think, that Maupas has made such a mistake. Nussbaum also points out that at 26° to 28° C. the conditions were not favorable, as shown by the relatively small number (104) of eggs produced. The maximum number for this many individuals would be 250 eggs. The results may, therefore, have been due to insufficient nourishment rather than to temperature.

In another similar experiment Maupas got the same results. Thus, five young Hydratina females laid their first eggs at a temperature of 14° to 28° C. Twenty-four per cent of these eggs produced individuals that laid male eggs, and 76 per cent produced individuals that laid female eggs. Five other individuals were kept at a higher temperature, 26° to 28° C., and laid 118 eggs, of which 81 per cent gave rise to individuals that produced male eggs and only 19 per cent produced individuals that laid female eggs.

Maupas found that under different conditions of temperature the same individual may at one time produce eggs that give rise to females that lay only female eggs, and at another time may produce eggs that give rise to individuals that lay only male eggs. The result shows that whether the egg becomes a male-producing or a female-producing individual is determined after it has been laid and not while it is in the ovary. Nussbaum's results show, in fact, that this is determined during the course of the first few hours after the individual hatches.

Maupas isolated six young females. They were kept in the

cold and laid there 34 eggs, of which 12 per cent only became individuals that laid male eggs and 88 per cent individuals that laid female eggs. The same parents were then transferred to a warmer temperature and laid 95 eggs that were male producers and 5 eggs that were female producers. They were changed back and forth from warmth to cold, and each time a corresponding change occurred in the individual that came from the eggs. During the last four days of their life they produced 50 eggs, of which 17 per cent were male-producing and 83 per cent female-producing.

Nussbaum has tried to show that the sex of the offspring is determined by the environment and not by influences on the egg. If the young parthenogenetic female after she has emerged is well fed, she produces large eggs that develop, without fertilization, into female individuals. If on the other hand an individual is at first poorly fed, she produces small eggs, and these develop without fertilization into males. Before and after this period the sex of the egg is not determined by the food supply, *i.e.* after the first egg has been laid it is no longer possible to change the sex of the other eggs.

Nussbaum thinks that Maupas was mistaken in regard to the influence of temperature, because he used too many individuals, whose numbers in proportion to the food supply determined the conditions of nutrition that exist. Maupas may also have judged the sex of the offspring from the size of the egg. This is not always possible, according to Nussbaum; for while it is true that the biggest eggs become females, and the smallest males, there are many of each kind whose sizes overlap.

Temperature favors the appearance of the males in so far as each animal lives at a higher rate at a higher temperature and needs more food, also at the higher temperature the output of eggs is faster, hence the food conditions poorer. At a lower temperature the output is slower and food conditions are relatively better; but since the kind of egg produced is determined before the first egg is laid, it is not obvious that this criticism is apropos.

Plenty of food during the development of the ovary leads to

female summer eggs. Early fecundation and scarcity of food during the time of development of the ovary lead to winter eggs, from which only females emerge.

Lauterborn has found in another species of rotifer, Asplanchna, that the same individual may contain a winter egg and male embryos. This is strong evidence in favor of the view that the male eggs and the winter eggs are the same, as Maupas inferred for Hydatina. The result recalls the somewhat similar observations of Issakowitsch on daphnia, where, however, the winter egg and the males appear consecutively. Lauterborn, following Weismann's idea for the daphnias, thinks that in rotifers, other than Hydatina, external conditions do not determine the sequence of parthenogenetic and sexual generations. Each species has a more or less definite number of generations in the parthenogenetic part of its cycle, but he brings forward no experimental evidence in support of his conclusion.

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CHAPTER XXIII

THE LIFE-CYCLE OF SOME HYMENOPTEROUS INSECTS

It has been pointed out that in some cases parthenogenetic generations alternate with sexual ones, the last parthenogenetic generation giving rise both to male and female sexual forms. In other cases, unfertilized eggs may produce only one kind of individual, usually the male, and in a few cases this may be the regular method of production of the male sex. The best-known case of this sort is that of the honey bee.

The queen bee leaves the hive, a few days after emerging from the royal cell, for her nuptial flight. She is followed by one or more drones, and union takes place in the air. Her receptacle becomes filled with sperm, and this supply lasts her for the rest of her life, that may extend over three or four years. The spermatozoa must remain alive during all this time, yet the oldest produce the same effect, so far as sex is concerned, as do the youngest. The receptacle, or spermatheca as it is called, opens by a short tube into the oviduct. It has a muscular wall, and a few of the spermatozoa are supposed to be squeezed out as the egg passes the opening — at least in the case of eggs that are to become fertilized.

A queen may produce half a million eggs in the course of her life, and must receive, therefore, at least as many spermatozoa, and probably more, since it is not improbable that several or many are set free for each egg. The eggs are deposited in the brood cells or chambers of the comb that have been prepared by the workers. The queen thrusts her abdomen to the bottom of each cell, and deposits there an egg, that is attached at the end opposite to the micropyle, or opening through which the spermatozoön enters. There are three kinds of brood chambers:

the worker cells that are very numerous; the drone cells that are much fewer in number; and the royal cells, of which there are, as a rule, only a very few. It has been shown both by direct observation and by experiment that the eggs laid in worker cells and in the royal cells are fertilized. These eggs produce females only. In the worker, the female sexual organs never fully develop. The eggs laid in the drone cells are unfertilized, and give rise to the drones or males. Rarely a queen may make a mistake and lay a fertilized egg in a drone cell, where it becomes a worker; or lay a drone egg in a worker cell, where it becomes a drone. Evidently, then, the sex is not determined by the character of the cell, but by the presence or absence of the spermatozoön.

A worker egg can be changed into a queen if the young larva is supplied with the food given to the young queens. This can be accomplished artificially by placing some of the royal jelly taken from a royal cell (where it exists in excess) in a worker cell, containing a young maggot not more than a day or two old. The bees will then continue to supply this cell with the royal jelly, and will break down the neighboring cells, destroying their inmates and thus make a larger, royal cell around this *nouveau riche* member of royalty. A drone egg cannot be changed into a worker or into a queen, although an exceptionally large male may be produced by feeding on the royal nutriment.

When a queen has become old and has used up all of the sperm in the spermatheca, she can produce only drone bees. Also when a young queen is prevented from leaving the hive she produces only drones; for it appears that union with the males cannot take place within the hive. Workers also have been known at times to lay eggs which produce only drones. These and other facts led Dzierzon, in 1845, to formulate his famous theory. The substance of his view has already been given. He stated that a queen must be fecundated if she is to produce new queens and workers; that drone eggs are not fertilized; but that worker eggs and queen eggs are always fertilized. Dzierzon also discovered that during copulation the eggs in the ovary

are not directly fertilized, but the seminal fluid is stored up in the receptacle, and this supply, once received, must serve for all subsequent fertilizations. Dzierzon thought that the queen has the power of determining at will whether an egg is to become fertilized or not, and determines thereby the sex of the individual. He thought that all the eggs in the ovary are alike, and the sex of the individual is determined by the occurrence or absence of fertilization.

The theory of Dzierzon has been much discussed, and while its main facts have been confirmed there have not been lacking those who have disputed one or another of its postulates.

It was soon appreciated that the theory could be tested if the queen of one race is fecundated by the male of another race; for according to the theory the queens and workers that are produced by such a queen should be hybrids, but the males should belong to the pure maternal race. Thus if a virgin Italian queen is put into a hive of German bees, lacking their own queen, the new queen may be fecundated by a German male. Her female offspring, queens and workers, will be hybrids; but her male offspring, the drones, will be pure Italians. Dzierzon himself found one instance that was an apparent exception, and so great was his confidence in this test that he gave up, for a time, his own theory, although later he appears to have returned to it from the confirmatory results of v. Berlepsch and v. Siebold.

This hybridizing experiment has been a source of contention down to the present day, and well serves to illustrate how many dangers may lurk in even a comparatively simple experiment. Some of the objections to the theory may now be briefly considered. It appears that in some cases the drones are like the hybrids, or even like the male, presumptively not their father, that fertilized the queen. Thus Perez found that after introducing an Italian queen fertilized by a French drone into a French hive, she produced 300 drones of which 5 were pure Italians, 83 pure French, and 66 were hybrids. The result proved, he thought, that the drones were hybrids. Similar cases have been described by other observers. The results seem to be

incompatible with Dzierzon's theory; yet several explanations have been offered to account for these exceptional cases, for it is generally admitted that they are exceptional and do not represent what usually takes place.

In the first place, the pedigree of the queen may not have been above suspicion, and consequently some of her offspring may show traces of their mixed origin. It is said that at the present time the domesticated races of bees have been so often crossed that it is difficult to obtain a pure individual. In any particular instance the matter could be easily tested by rearing sister queens of the same brood, crossing one and breeding the other true. This simple test does not appear to have been made.

In the second place, the hybrid drones may have come from the hybrid workers that sometimes lay eggs, rarely in the common hive bees, but more often in the Syrian and Palestine races. In the third place, it has been found that Italian bees of presumably pure stock often produce drones that are very variable in their markings. In a recent paper by Casteel and Phillips it has been pointed out that the males are often more variable than the workers — a fact of much biological interest in itself, aside from the present question, since it shows that variation is not necessarily connected with the union of two germ-cells from different individuals, as Weismann and his school have assumed.

In another way Dzierzon's theory was tested, and apparently found wanting. Landois (1867) put worker eggs into drone cells, and drones were produced. Conversely he put drone eggs into worker cells and workers were produced. The real explanation of this result is, however, not that the kind of cell determines the sex of the individual, as the experiment seemed to show, but that the bees themselves often clean out a cell into which an egg has been introduced, perhaps because of the imperfect method of fixation of the egg, and subsequently the queen will deposit the proper kind of egg in the cell. Thus the bees themselves easily defeated the purpose of the experiment. The experiment could be properly carried out by removing the queen when the transfer is made, so that no

opportunity is left to deposit new eggs in the cells, if the workers remove them.

In recent years an apiarist, Dickel of Darmstadt, has claimed to have discovered facts that contradict the Dzierzon theory, and his contention, although it appears ill-founded, has led to a re-examination of the theory. He has tried to show that drone eggs as well as queen and worker eggs are fertilized, and that the sex is determined by the treatment to which the eggs are subjected by the workers. He admits that males may come from unfertilized eggs of queens and of workers, but he calls these false drones that are incapable of procreation. He believes that before fertilization the egg contains only the male elements. The sperm cell contains only female elements. After union these sexual elements are equally balanced, and the fate of the embryo is determined by the following external factors. In making the brood cells the wax is kneaded in the mouths of the workers, and impregnated with the saliva. The kind of saliva used is different for the drone and for the worker cells, and its presence in the walls of these cells determines the kind of secretion that is poured over the egg by the workers when it is laid. This secretion determines the sex of the egg. One kind of saliva is used for the queen larva, and causes a fertile female to develop; another kind causes the male to develop. If both of these are put into the same cell, they retard the development of the sexual organs and a worker is produced. There is also another nourishing secretion that is used for all kinds of larvæ, and does not affect the sex. Dickel tried to show by transferring drone eggs to worker cells, and *vice versa*, that the sex of the young larva can be changed by the change in food that the bees give to it in a foreign cell. The experiment is open to the criticism mentioned above, namely, that the workers may remove the egg, although the possibility might be very simply tested by removing the queen.

This ingenious and highly speculative, not to say fanciful, idea of Dickel has so little in its favor in the way of scientific evidence, and so much opposed to it that seems fairly well

established, that it need scarcely be discussed seriously. Petrunkewitsch has severely criticised Dickel's views, and has pointed out that the supposed experimental proofs are all open to question; that his ideas in regard to fertilization are hazy; and that a renewed investigation by means of the more perfect modern technique has confirmed v. Siebold's and Leuckart's statements that spermatozoa are not present in drone eggs. For instance, Petrunkewitsch found the sperm nucleus in 23 out of 29 eggs from worker cells. On the other hand, of 94 eggs from drone cells not one contained a spermatozoön. These eggs were in the stage when the first polar body was present. In the following cases the second polar body was forming:— 62 eggs from worker cells all contained sperm asters, while 272 from drone cells contained no asters, except in one case. It may be that in this one case the queen had erred and placed a fertilized egg in a drone-cell, which is supposed to occasionally occur. These results furnish a further confirmation of Dzierzon's theory.

Other Hymenoptera

The ants are closely related to the bees and show apparently similar conditions in regard to the determination of sex. It has long been claimed that the unfertilized eggs of the queen and the unfertilized eggs of the workers produce males. Hence Dierzon's theory has been extended to this group also.

In the last few years, however, some cases have been recorded that seem to show that workers may appear in nests that have no queen, and which, therefore, have come from workers' eggs, which are never, as far as known, fertilized. The seminal receptacle is absent in the workers, hence there would be no opportunity for the storage of sperm, and since in one case workers appeared during three years, they must have come from parthenogenetic eggs.

Wheeler has recently brought together the best authenticated cases of this kind. Tanner records for Atta cepholotes that a group of worker ants in an artificial colony produced eggs most

of which were males, but two queens also appeared. Reichenbach started with eleven workers of Lasius niger. They laid eggs that became typical workers. In August, when the sexual forms appeared in the out-of-door nests, about a dozen males also developed in the artificial nest, although none had developed before. After a few weeks the ants continued to increase in numbers, and in the following year produced two to three dozen males and as many as 300 workers. The same appearance of males took place in the third year.

Another case has been given by Mrs. Comstock for Lasius niger in which workers appeared in an artificial nest containing only workers. The queen of this species is so much larger than the workers that a mistake as to the character of the individuals was not possible.

In another group of the Hymenopterous insects, the Tenthredinidæ, or sawflies, some curious cases of parthenogenesis are known. As a rule, in this group the males are much less numerous than the females. The common currant sawfly, Nematus ribesii, produces parthenogenetic progeny which is nearly always of the male sex. It is said that on rare occasions an unfertilized egg becomes a female, a point of some interest in connection with the case of the bees.

Doncaster has recently given some observations of his own, and reviewed the results of others in regard to the sex of sawflies from parthenogenetic eggs. He points out that according to all observers females alone arise from virgin eggs of Crœsus varus and Pæcilosoma luteolum, only one observer ever having seen a male. He quotes Mrs. Chawner to the effect that she has bred thousands of the latter species for several years in succession without obtaining males, and without finding any diminution in the fertility of the females. Hemichroa rufa "is known to give chiefly females from virgin eggs, but occasionally males are produced." On the other hand, certain species produce males, as a rule, from parthenogenetic eggs. Cameron states that Nematus pavidus yields only males from unfertilized eggs. In Nematus ribesii (N. ventricosus of von Siebold) it has generally

been found that virgin eggs produce males, but von Siebold obtained 13 females among 1700 males; he thinks these may have been introduced with the food. "Other observers have obtained only males."

In another group, the gallflies, Cynipidæ, females appear in preponderating numbers and reproduce by parthenogenesis in one generation at least. Males in some forms are of the rarest occurrence, and have never been found in some species. It has been observed, however, that in some species the eggs produced by the parthenogenetic females give rise to insects, both male and female, quite different in appearance from the parthenogenetic generation. The complete life histories of some of these species have been given on page 268 in describing the formation of galls. According to Adler, not more than 2 per cent of males appear in the sexual generation of Rhodites rosæ and R. eglantenæ. The female of Phromali lays her egg in the caterpillar of Vanessa urticæ. In several cases caterpillars were reared, which were kept uncontaminated, and an unfertilized female of Phromali deposited eggs in them. When the flies emerged from the pupa there were found in one case 124 males, in another case 62 males, in a third case 75 males and 5 females, and in a fourth case 45 males and 4 females. Thus while the unfertilized eggs of this species produce males, occasionally females also appear.

These cases serve as a warning not to insist with too much positiveness on the view that in the bee unfertilized eggs always produce males, since they show that exceptions to such a rule may sometimes occur.

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EXPERIMENTAL STUDY OF THE DETERMINATION OF SEX

CHAPTER XXIV

THE DETERMINATION OF SEX

Introduction: the Different Kinds of Sexual Individuals

FEW questions in biology have attracted more interest than that of the determination of sex. Blumenbach, in his fascinating brochure, "Ueber den Bildungstrieb," points out that Drelincourt brought together two hundred and sixty-two groundless hypotheses of sex that had been proposed, and Blumenbach remarks quaintly that nothing is more certain than that Drelincourt's own theory made the two hundred and sixty-third. In recent years a large number of facts bearing on the determination of sex have been brought together, and yet the question remains as much a puzzle as it was in the time of Drelincourt and Blumenbach.

Before attacking the main question of the determination of sex let us consider the different kinds of sexual individuals found in the animal kingdom. By sexual individuals we mean those forms that reproduce themselves by eggs and sperm in contrast to reproduction by budding, or by division, or by spores; but while this distinction will hold in most cases, it is an arbitrary distinction, since we recognize sexual reproduction in the protozoa, where entire individuals unite or even fuse, and the distinction between a spore and a parthenogenetic egg depends largely upon what we suppose to have been the historic origin of these two kinds of reproductive cells, rather than on any inherent difference in the cells themselves.[1]

[1] One or even two polar bodies are given off from parthenogenetic eggs, but not from spores. The bearing of this difference on the sexual problem is unknown. It is not necessarily connected with a reduction on the number of chromosomes.

Individuals of two kinds exist in many species of animals, — males and females. Such *individuals* are said to be unisexual, and the *species* diœcious (or of two households). In other species there is only a single kind of individual that produces both eggs and spermatozoa. Such individuals are bisexual or hermaphroditic; and the species is said to be monœcious (or of one household). Closely related species may belong to the one or to the other of these two groups, so that the distinction does not appear to be of fundamental importance. Moreover, individuals sometimes appear in diœcious species that are hermaphroditic; and, conversely, individuals of separate sexes sometimes appear in monœcious species. The prevailing view is probably correct, that male individuals carry in a latent or potential condition the female characters, and the female those of the male. If the latent character develops, an hermaphrodite appears; and if, in a monœcious species, one set of characters fails to develop, a male or a female appears. From this point of view we can readily understand how easily the transition from one to the other kind of sexual individual may take place.

A third kind of individual is also recognized, namely, the parthenogenetic. Such an individual is looked upon as a female, in which the eggs have the power to develop without fertilization. This may sometimes happen in ordinary females, so that parthenogenetic reproduction is not sharply separated from sexual reproduction. Even in the same individual, as we have seen in the case of the bee, the eggs may develop with or without fertilization. Since parthenogenetic individuals may produce males as well as sexual females, we must conclude that the male characters are carried in a latent condition by these parthenogenetic females, often through a long series of purely parthenogenetic generations. The possibility that there might be male and female lines of such parthenogenetic females is excluded by finding that the same individual may produce both males and females, as seen in aphids and daphnia.

Diœcious Species, composed of Unisexual Individuals

When the species consists of male and female individuals, we find in some cases that the sexes are so much alike externally, that without a knowledge of their internal structure we could not tell them apart. Some birds, pigeons, for example, belong to this class, and there are even some mammals, mice for instance, in which the sexes are so closely similar that an inspection of the external organs of reproduction is necessary to reveal the sex. In many other cases the external differences involve mainly the external organs of reproduction, while in still other groups the whole form of the body may be different, and in extreme cases this difference is so great that were not the relation of the individuals known they would be placed in different species.

Where the sexes are separate it may be said to be the *rule* for equal numbers of males and females to exist, but this rule is far from invariable.

In regard to the human race, statistics from the whole of Europe, including records of "millions" of births, show that for every 100 female children born there are 106 males. If a more limited range is taken, or a shorter period, some deviations from this proportion are found.

Thus between the years 1887–1895 the following ratio of the sexes to each other is given by Bodio: —

	Males	
Italy	105.8	to 100 females
France	104.6	
England	103.6	
Germany	105.2	
Austria	105.8	
Hungary	105.0	
Switzerland	104.5	
Belgium	104.5	
Holland	105 5	
Spain	108 3	
Russia	105.4	

Thus, despite the different conditions, social and political, in different countries, the proportion remains nearly the same.

These figures give the birth rate. The proportion differs considerably from the proportion of adult males to females; for in Europe, for example, there are 1000 men to every 1024 women. Thus the adult proportion is the reverse of the proportion at birth; or, in other words, the excess of males at birth is more than made up by the greater death rate of boys as compared with that of girls.

Local conditions also affect the proportion, for in Italy and in the Balkan Peninsula there are more men than women. As stated, the death rate of male children in Europe is known to be greater than that of female children. At about the twelfth to the fifteenth year the numbers become equal. After the thirty-fifth year the men die oftener than the women, which finally brings about the conditions mentioned above. Male children appear less resistant than female, and adult males die more often from greater exposure to danger, from alcoholism, and from crime, etc.

For animals the following records have been collected by Lenhossek: —

	Males	Females
Horse	98.31	100 (Dusing)
Cattle	107.3	100 (Wilchens)
Sheep	97.7	100 (Irwin)
Pig	111.8	100 (Wilchens)
Rat	105.0	100 (Cuénot)
Dove	105.0	100 (Cuénot)
Hen	94.7	100 (Darwin)
Grassfrog	82.0	100 (Cuénot)
Fly	96.0	100 (Cuénot)

There are some other remarkable cases in the vertebrates. Pflüger found the disproportion between male and female frogs reared from eggs to be astonishingly great. This led him to examine the proportion of adult males and females in the

localities from which he obtained the eggs, with the following results: —

	Prop. in Nature		Obtained artificially	
	Male	Female	Male	Female
Utrecht	13.2	100	18.1	100
Bonn	36.6	100	35.7	100
Königsberg	46 7	100	48.5	100

The meaning of the enormous difference is by no means clear. Lenhossek has suggested that if the Utrecht egg were to be fertilized with sperm from the Königsberg race, and *vice versa*, interesting results in regard to whether the egg or the spermatozoön determines the sex might be obtained.

Geddes and Thomson state that in fishes the females are usually more numerous than the males, never less so, except in anglers and catfish. They give the following data: —

	Female		Male
Flounder	1	to	1
Roughead	12	to	1
Cod	3	to	2
Gurnard	9	to	2

There is a further point of some importance in regard to man, namely, the proportion of males and females that occur in abortive births and of still-born infants. The statistics show that a much larger number of these are males. Thus Rauber found the proportion for 57 embryos was 159 males to 100 females. Lenhossek examined 156 embryos (between the third and sixth month), and found the proportion to be 160 males and 100 females.

For still-born infants, fully formed, but not alive, the following figures have been given: —

Quetelet found 133.5 males to 100 females; Bodio gives: —

	Males	
Italy	131.1	to 100 females
France	142.2	
Germany	128 3	
Austria	132.1	
Hungary	130.0	
Switzerland	135.0	
Belgium	132.0	
Holland	127.1	
Sweden	135.0	
Norway	124.6	
Denmark	132.0	

From these results it is clear that the proportion of male to female embryos is distinctly in favor of the males. The meaning of this is unknown.

Monœcious Species, composed of Bisexual or Hermaphrodite Individuals

Since the groups of animals with which we are most familiar, the vertebrates, insects, and higher crustaceans, are composed of individuals with separate sexes, we are apt to forget how often in other groups the sexes, or more accurately the sex-cells, are united in the same individual. In the following list some of the groups are given in which hermaphrodite individuals exist: —

Sponges, sexes separate or united.
Cœlenterates, sexes separate or united.
Flatworms, sexes united, a few cases of separate sexes.
Nemerteans, sexes rarely united. Separate sexes the rule.
Nematodes, sexes separate as a rule, but united in some cases.
Annelids, sexes united in earthworms, separate in marine worms (except Protodrilus).
Crustacea, sexes separate, but united in some barnacles.
Mollusca, sexes separate in some, united in other groups.
Echinoderms, sexes separate, united in a few cases.

Thus in the greater number of the great groups, hermaphro-

ditism is found, although in only one of these, the flatworms, is it the almost exclusive condition.

It would be interesting to take up these groups in turn and examine the relation of the two kinds of sexual individuals, but I shall select only one group in which the relations are especially instructive, although exceptional.

In the group of Nematodes, or round worms, we find a curious case of alternation of two kinds of sexual individuals. Ascaris nigrovenosa is an hermaphrodite form found in the lungs of frogs. The eggs pass through the digestive tract of the frog and hatch as the Rhabditis form that has separate sexes. Equally remarkable are the cases in which there exists an hermaphrodite form that appears to represent the female individual in which secondarily spermatozoa as well as eggs have developed. Maupas has studied these species with great care, and I follow his description.

Maupas points out that there have been described 34 species of Nematodes in which reproduction without males has been established; of these 34 species 25 are hermaphroditic and 9 parthenogenetic.[1] Of the 34 species, 16 belong to one genus Rhabditis. We are concerned here only with the hermaphroditic species. These forms differ in no bodily character from the females of other species with separate sexes, and differ only in the ordinary specific differences. A minute study of their sexual organs at the time of maturity is necessary to detect their hermaphroditic character. It is found that when the reproductive organ is fully formed, it functions first as a testis. The germ-cells at the anterior end of the ovary begin to divide rapidly and become small spermatozoa. These are stored up in a receptacle of the uterus. Later other cells, also situated at the anterior end of the ovary, begin to grow larger; they store up yolk, and become large eggs. They enter the uterus and become fertilized by their "own" spermatozoa.

[1] This list Maupas says will probably be augmented, for of the 206 species that are known from fresh water and from land, 85 are known only by the females.

In some species the females have neither the "disposition" to unite with male individuals nor the apparatus for storing the sperm. Males occur in some of these cases, but they also often lack the sexual instinct, and their spermatozoa are condemned to perish.

Another point of great interest has been made out by Maupas, viz., the imperfection or insufficiency of the hermaphroditism. More eggs are produced than there are spermatozoa present to fertilize them. Those that are first set free from the ovary become fertilized, the rest become rapidly disorganized. The number of fertilized eggs produced by a well-nourished individual is only about 200 to 250.[1] This condition is far from being an advantage to the species, for if separate sexes existed, at least 800 eggs might be fertilized. If only half of these eggs produced females, still the number would be 400, which is larger than the number of individuals produced by the hermaphroditic species. In the second generation there would be 160,000 individuals from the unisexual females, but only 60,000 hermaphroditic females. Thus there is no reason to suppose that this hermaphroditic condition is the result of an adaptation of the species. Instead of an advantage it is a process injurious to the species, but suffices, nevertheless, to keep it in existence.

Males appear in these hermaphroditic species, but in relatively small numbers. Maupas has given the proportions observed in the following table: —

Diplogaster robustus	0.13 males	to 1000 females
Rhabditis guignardi	0.15 males	
Rhabditis dulichura	0.7 males	
Rhabditis caussaneli	1.4 males	
Rhabditis elyaus	1.5 males	
Rhabditis coronata	5.0 males	
Rhabditis perrieri	7.0 males	
Rhabditis marionii	7.6 males	
Rhabditis duthiersi	20.0 males	
Rhabditis viguieri	45.0 males	

[1] In one species only, Rhabditis guignardi, there are more, namely, from 520 to 530.

This means that in Diplogaster robustus there is 1 male to 10,000 females, and in Rhibiditis viguieri 1 male to 450 females.

There is nothing in the structure or in the organization of these superfluous males that would lead us to consider them imperfect. In every point of their organization they correspond to the ordinary type of the males of unisexual species. Even the testis is normal and produces spermatozoa which are identical in form, size, and structure with those in the hermaphroditic glands of the corresponding females. On the other hand, these males have nearly lost their sexual instincts, and are rarely seen to pair with the hermaphroditic females.

Maupas carried out the following experiments. He placed males and females together for a number of days and recorded the number of times fecundation took place. It will be observed that more that half of the cases occurred in Rhabditis marionis, in which it is known that the hermaphroditism is incomplete.

	Females	Males	Fecundations	Days
Rhoditis elegans	139	112	6	4 to 9
Rhoditis caussaneli	42	35	0	5 to 10
Rhoditis marionis	28	42	13	5 to 7
Rhoditis duthiersi	62	41	1	4 to 6
Rhoditis perrieri	26	35	0	5 to 7
Rhoditis duthiersi	12	5	0	6 to 7
Diplogaster robustus	4	2	0	4 to 5
	313	272	20	

Thus 313 females put with 272 males gave only 20 fecundated females. In all cases except R. marionis the sexual indifference of the males is almost absolute. This is the more surprising, since in other species of Nematodes with separate sexes the copulation is readily observed and lasts for some time. Here, then, we have a case of a psychical "decadence," unaccompanied by structural degeneration. The sexual process is being replaced by hermaphrodite fecundation.

This elimination of the male type in the Nematodes is shown

by the series of species showing intermediate stages. Incomplete females are found in which one ovary alone produces both kinds of germ-cells, the other only the female germ-cells, and still other individuals are hermaphroditic in both ovaries.

Parthenogenetic Species

Parthenogenesis is also of not infrequent occurrence in the animal kingdom. It is found most often in insects and in the lower crustaceans and rotifers. It is found in some Nematodes [1] and in a few other groups. In many cases the eggs of unisexual forms may begin their development if not fertilized, and in recent years it has been shown that parthenogenetic development may be induced artificially in many species of animals. Thus we have come to look upon the egg as capable of producing an embryo if the proper external stimulus to development is present. In nature this process has been carried out quite often with far greater success than has been as yet accomplished by artificial means.

In some cases, as in the aphids, the parthenogenetic females (wingless or winged) can be distinguished structurally from the egg-laying females. The latter alone have the receptaculum seminalis for storing the sperm. In other cases the two kinds of females may be, externally at least, almost identical. The ova are, however, sometimes different, as in daphnia.

Since the eggs of so many species show incipient parthenogenesis, we have come to regard natural parthenogenesis as having arisen by the disappearance of the males in certain generations. The rareness of the males in certain groups in which parthenogenesis has replaced the sexual modes of reproduction — in some rotifers, sawflies, etc. — seems to support this point of view. The question is, however, not quite so simple as this if we examine it more closely. What has become of the male eggs if this view is correct? Do they simply fail to develop, or have they become female eggs? There is no evidence to show that half

[1] Maupas records seven parthenogenetic species in the Nematodes.

of the eggs (those that formerly produced males, let us say) are present and fail to develop. The alternative view seems more plausible, that all the eggs produce females. If this view is the correct one, then we find that in parthenogenetic species two changes have occurred, all the eggs produce females, and at the same time these female eggs have acquired the power to develop without fertilization. It may be that both processes have gone on hand in hand, and the same tendency to develop parthenogenetically is associated with a tendency to produce only females. In not a single case has the sex of the embryo, produced by artificial means, been determined, therefore we lack experimental evidence to form any opinion on this point. In species where occasional parthenogenesis occurs both male and female individuals may develop from unfertilized eggs, as in the silkworm moth. In other groups apparently more females develop, as in certain other moths, but in these the process of parthenogenesis is sometimes quite regular rather than occasional. In the honey bee and in some other hymenoptera, males as a rule develop from parthenogenetic eggs.

Whatever conclusion we reach finally in regard to the origin of parthenogenetic species, one point must be always borne in mind: parthenogenetic eggs carry latent, or in a potential condition, the male characters which may at any time become dominant. There are certain species that produce only parthenogenetic females in one generation, but males and females in approximately equal numbers may appear in the next generation, as in the gallflies; and in other species that have a long succession of parthenogenetic females, males and sexual females may appear in at least equal numbers. These cases seem to indicate with some probability that parthenogenesis has not arisen by the suppression of the male eggs, but by the dominance of the female characters in all of the eggs. What is true for the so-called female eggs is probably also true for the male-producing eggs in unisexual forms. The male egg carries latent the characters of the female, and the hereditary transmission by means of the male of the maternal characters shows that this must be the true view.

In certain moths, Solenobia triquelrella and S. lichenella and Psyche helix, a succession of parthenogenetic females has been known to occur. In the first two species males may not appear for years, and then suddenly appear, and even excede the females in numbers. In one group of Rotifers, Philodinidæ, males have never been found. In other families small, semi-parasitic males may be present, but it is believed that in some of these cases these minute males do not fertilize the eggs. Whether the males have thus slowly disappeared or have suddenly ceased to appear in the Philodinidæ is not known or even surmised.

In still other insects parthenogenesis occurs. The larva of the fly, Miastor, produces eggs that develop within its body and produce there young maggots. This method may go on for several generations, but ultimately some of the larvæ pupate and the sexually perfect flies emerge. The conditions that determine which mode of production takes place have not been determined. In the gnats of the genus Chironomus, the pupa deposits eggs, but the pupa is in reality an imago that does not ordinarily leave its pupa skin. Thrips seem to reproduce by parthenogenesis throughout a part of the year. Some caddis flies are said to be parthenogenetic. The walking sticks of the genus Bacillus also produce as a rule by parthenogenesis. In Bacillus Rosii only 1 male and 20 females were found to emerge in one case from parthenogenetic eggs. In some moths and butterflies, parthenogenesis occurs either as a regular or as an occasional process. Parthenogenesis has already been described in the gallflies, and other cases in the hymenoptera will be described later. In other groups of animals, parthenogenesis is also known, as in the Trematodes, for instance; but the group of insects furnishes the most striking cases of this method of reproduction.

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CHAPTER XXV

EXTERNAL FACTORS OF SEX DETERMINATION

WHETHER the sex of an individual is determined by external factors during the course of development, or whether the sex is already determined in the egg, has been the subject of much discussion. I shall first consider the experimental evidence that has seemed to show that external conditions may determine sex, and then examine the evidence in favor of the view that sex is predetermined in the egg, either before or after fertilization.

Influence of Food

Of the different external factors that have been supposed to determine the sex of the individual, nutrition occupies the first place. Nutrition is supposed in some cases to influence the sex of the young animal, while in other cases the egg itself is supposed to have been affected by the condition of nutrition of the mother.

The work of Landois in 1867 was the first in the field. He stated that he could produce, at will, males or females, of the butterfly Vanessa urticæ by regulating the amount of food. Six years later Mrs. Treat claimed to have obtained similar results, and in the same year, 1873, Gentry made a statement to the same effect. Mrs. Treat made use of the caterpillars of Papilio asterias. One lot deprived of food before the last moult gave 34 males and 1 female. Another lot, well fed, gave 68 females and 4 males.

Riley carried out, in 1873, a more thorough series of experiments on the same species, as well as on others. He tried especially the effects of starving the caterpillars, for he says that it is not possible to make caterpillars take more food than they do naturally, and under this condition they produce both males

and females. The starved caterpillars gave no special excess of males, although there were, it is true, a few more males; but Riley pointed out that under natural conditions the females in several species take a longer time than do the males to reach the pupa stage, undergoing in some cases one more moult, so that, if starved, the mortality would therefore probably be greater amongst the females, and hence more male than female moths might be found. Other observers, Bessels 1868, Briggs 1871, Andrews 1873, Fletcher 1874, have also found that an excess or diminution of the food does not alter the proportion of the sexes.

The futility of many of these experiments has now become apparent, since it has been shown that the sex of the caterpillar is already determined when it leaves the egg. Under these circumstances it is not probable that feeding could produce a change in the sex. It is much more probable that starvation or overfeeding could only effect the proportion of males and females by bringing about a greater mortality of the individuals of one sex.

Kellogg and Bell have studied food conditions in relation to sex determination in silkworms (Bombyx mori). They have guarded against the possibility of greater mortality of one sex. The chief interest of their work is their examination of the possible effects of nourishment on the second generation. The effects of feeding the caterpillars themselves different amounts of food were as follows. Twenty larvæ were present at first in each lot.

"Lot I. Fed optimum food; no deaths before emergence of moths; produced 8 males, 12 females.

"Lot II. Fed optimum food; 2 deaths before maturity; produced 7 males, 11 females.

"Lot III. Fed one half (approximately) of optimum of food; 4 deaths before maturity; produced 10 males, 6 females.

"Lot IV. Fed living minimum of food; 3 deaths before maturity; produced 10 males, 7 females.

"Lot V. Fed living minimum of food; 6 deaths; produced 9 males, 5 females."

The results seem to show a slightly larger number of females in the well-fed lots, and a larger number of males in the starved sets; but the numbers are too small to justify any conclusions from them, and those that die may have altered the proportions. In other experiments the authors found that the results do not lead to any conclusions in regard to the influence of nourishment.

The possible influence of food in determining the sex of the egg (or sperm) was also examined. In the following table those larvæ that had the optimum amount of food are indicated by O. Those that had a minimum of food are indicated by M. The amount of food given to the grandparents, to the parents (third column), and to the larvæ themselves (second column) is indicated by the letters.

Lots	Fed	Parents	Grand-parents	Deaths before Maturity	Males	Females
1	O	O	O	2	13	10
2	M	O	O	2	14	9
3	O	M	O	3	8	14
4	M	M	O	6	8	11
5	M	O	M	O	15	10
6	M	O	M	O	11	14
7	O	M	M	20	2	3
8	M	M	M	21	2	2

It is not evident from these data that the sex of the egg is influenced by the condition of the parents or grandparents.

Cuénot has carried out in recent years some important experiments with moths and flies. When the caterpillars of Ocneria dispar were given an abundant nourishment, they produced 52 females and 4 males. Caterpillars of Bombyx rubi were given so small an amount of food that great mortality resulted. Of the 27 survivors there were 13 males and 14 females.

Cuénot states that in the maggots of flies, the gonads, although present in young larvæ, do not undergo their histological differentiation until a relatively late period of larval life, hence there might appear a better opportunity to influence the sex,

provided, of course, that it is not in reality already determined, since the absence of differentiation of the sex cells does not necessarily mean that the sex may not have been previously settled. Lowne had found that flies from large larvæ are almost always females, and those from small larvæ males; but Lowne himself doubted the value of his observations, and Cuénot says his conclusion from them is erroneous. Weismann fed one lot of Calliphora vomitoria abundantly, and starved another lot from time to time. Both lots produced males and females. Cuénot's experiments were as follows: —

Experiment I. The larvæ after hatching were fed abundantly on putrefying flesh, and produced large flies. The proportion of females to males is given in the next table.

			Per Cent of Females
Lucilia cæsar	273 females	281 males	49.0
Calliphora vomitoria	224 females	215 males	51.0
Sarcophaga carnaria	96 females	90 males	51.6

Experiment II. The larvæ were given as little nourishment as possible; they often were entirely without food, and the mortality was very great. The flies were small. The proportion of females to males was as follows: —

			Per Cent of Females
Lucilia cæsar	95 females	69 males	57.92
Calliphora vomitoria	93 females	91 males	50.05
Curtonevra pabulorum	26 females	17 males	50.50

Experiment III. The larvæ were kept under varied conditions, being fed on brain, suet, and a little meat. They were in a starved condition at first and were then abundantly fed or were fed at first and then starved. Several species were reared together.

Calliphora vomitoria (April 19)	185 females	166 males
Lucilia cæsar (Aug.–Sept.)	143 females	141 males

The normal proportion of males to females in these species of flies is approximately equal. This relation is also found in those kept under the different conditions of the other experi-

ments. Cuénot concludes, therefore, that sex is not determined by external conditions, but is predetermined in the egg.

The question turns, therefore, on what condition determines the sex of the egg. Can the nutrition of the parents during the larval stages affect the proportion of male and female eggs? Cuénot carried out some experiments to test this possibility.

Experiment I. Larvæ of Calliphora vomitoria, that had been poorly nourished from the time of hatching, produced 12 males and 5 females that were not more than half the normal size. The flies were inclosed in a cage and fed on sugar and meat. They laid 20 lots of eggs. The larvæ that hatched were fed and produced 359 females and 353 males. No influence due to the starved condition of their parents was observed.

Experiment II. Adult flies of Calliphora vomitoria that had hibernated in the laboratory all winter without food were captured in March and April. They were fed on sugar and meat, and then laid 7 lots of eggs. The larvæ were well fed and produced 306 females and 308 males. This result also shows that the condition of the parents is without effect on the sex of the offspring.

Pictet has recorded the proportion of males and females that appear when the food of caterpillars is different from the normal. The general effects of the change of diet was in some cases to give insufficient nourishment, in other cases more nourishment than supplied by the normal food. The results seem to show that when the food is insufficient the proportion of males is greater. Thus Ocneria dispar fed on walnut leaves gave in the first generation 54 males to 46 females, and in the second generation 65 males to 35 females. When the first generation was fed on walnut leaves and the second on oak leaves (the normal food), there were 61 males to 39 females. When the first generation was fed on walnut, the second on oak, and the third on walnut again, there were 65 males to 35 females.

Esparcette and dandylion furnish an ample supply of nourishment; the former gave in the first generation 51 males to 49 females, and the latter 52 males to 48 females.

Thus while poor nourishment increases the percentage of males, good nourishment does not increase the percentage of females above the normal. The results may be due, Pictet admits, to mortality rather than to a change in sex affected by the food.

A number of experiments have been carried out with tadpoles of frogs. An observation made by Born seemed to him to show that the sex of the tadpole of the frog is determined by the amount or by the kind of food eaten by the young animal. He found that when the tadpoles of Rana temporaria (from eggs artificially fertilized) were fed on a mixed vegetable and meat diet, that 95 per cent of them were females and 5 per cent were males. This was a general result obtained from several lots of 1443 tadpoles in all. In some aquaria all the individuals were females.

The experiments of Yung (1883) are more discriminating. He fed tadpoles of Rana esculenta on different kinds of food. In one lot (A) the flesh of fish was given. These tadpoles were large and well developed. In another lot (B) the flesh of beef and of fish was used. These tadpoles were also large. In a third lot (C) the white of eggs was used. These tadpoles were smaller. In a fourth lot (D) the yolk of hen's egg was given. These tadpoles were even smaller than the last. The number of males and females that developed is shown in the following table: —

	No. of Young Frogs	Males	Females	Doubtful	Lost	Proportion of Females
Lot A (fish)	24	4	17	2	1	70 %
Lot B (fish and beef)	33	6	25	2	–	75 %
Lot C (white of egg)	10	3	7	–	1	70 %
Lot D (yolk of egg)	7	0	5	2	–	71 %

There are also a few other statements by other authors in regard to the influence of food. Thus Balbiani and Henneguy state that an excess of females is found in tadpoles fed on yolk

of egg [1] as compared with those that obtain only a vegetable diet.

These results on tadpoles have been shown to be inconclusive for the following reasons: — The method followed by Born of determining the sex of the tadpoles at their time of metamorphosis was very inexact. He relied on the size of the gonads (testis or ovary), but histological examination has shown that the female gonad is not always larger than the male, and there are always so many cases intermediate in size as to render the conclusions invalid. Even the method of teasing out the gonads, a method also used by Born, cannot be relied upon. Furthermore, unless the number of tadpoles that die is taken into account (and the number may be considerable), we cannot be certain that the results may not be due to greater mortality of one or the other sex under certain conditions. If further evidence were needed to invalidate these results, they are to be found in Pflüger's observations on the proportion of males and females in certain species of frogs. As already pointed out, the eggs from certain localities give a high percentage of females, and the same disproportion of adult frogs is found under natural conditions. It is true that this does not in itself show that the sex may not be determined by the external conditions; but if the natural disproportion of males to females is very great, error may easily creep into the experimental results.

The most important objections to the results of Born and of Yung are found in the more recent experiments of Cuénot. His results are as follows: The eggs of Rana temporaria were used. The first lot lived on a vegetable diet. They suffered from the confined space, and the tail was often malformed. Their development was retarded and the genital organs (gonads) were small. The 26 young that underwent metamorphosis were all females. In the second lot the conditions were the same as the last, and 3 females and 4 males were found. The third lot was kept in a large aquarium with cool, running water. The tails were cut off several times with the intention of prolonging thereby

[1] It is not clear that yolk of egg is a good food. See Yung's results.

the metamorphosis, which took place, in fact, — owing probably to the temperature, — two and a half to three months later than the others. Sections of the gonads showed 30 females, 26 males, and 1 hermaphrodite.

The fourth lot, fed for some days on the jelly of their own eggs, were separated into three groups. The results were as follows: —

	Males	Females	Not differentiated
Group I (vegetable food)	57	51	8
Group II (animal food)	22	14	0
Group III (mud and their own dead)	12	23	0

Groups I and II developed at the same rate. They were small, owing to the size of the aquarium, and underwent their metamorphosis at the beginning of June. Group III was retarded. The tadpoles were small and had begun to die at the beginning of June. They were then fed on an animal diet, when they began to grow rapidly, and metamorphosed at the end of July. The frogs were small, and yet as the table shows there were more females than males, while in the case of those of Group II that had animal food there are more males than females. In the case of Group I the two sexes are nearly equal in number.

Cuénot points out that his own results as well as those of others are open to the serious objection that the sex of those that died is unknown, nevertheless he thinks that his experiments show that food is not a factor in determining the sex of tadpoles.

The best-authenticated cases that seem to show the influence of food on the determination of sex are those of Hydatina senta and the daphnid, Simocephalus. The experiments that seem to establish this relation have been given in previous chapters. According to Nussbaum, the amount of food taken by Hydatina during the first few hours after hatching determines whether the kind of eggs laid will give rise to males or to females. This may mean either that all the eggs have their sex determined at this time, one way or the other, or that the food determines

whether female or male eggs develop, assuming both kinds to be present. As yet this point is unsettled. If Maupas's conclusion is correct, that the male eggs and the winter eggs are the same, fertilization or its absence determining their fate, it would seem that the same external conditions that produce a winter egg produce its potentially equivalent male egg. In Simocephalus lack of food causes either the male or the winter egg to develop. If Weismann's statement is correct, that the parthenogenetic egg and the winter egg come from different parts of the ovary, it may prove that the male egg and the winter egg are here also the same. This question needs, however, further examination.

Supposed Influence of Nourishment in Determining Sex in Man and Other Mammals

In the cases so far examined the eggs are laid immediately after fertilization, so that if their sex were not already determined by the parent, no further chance for such an influence exists. In man and in other mammals the embryo develops in the uterus of the parent, and the opportunity is afforded of influencing the sex, if such were possible, by the condition of nutrition of the parent. It has often been claimed that the sex of the child is determined in this way, and as often denied. The method employed in this case is to examine the statistics giving the proportion of males and females born of parents living under supposed favorable and unfavorable conditions of nutrition. It has been claimed that more boys are born in the poorer classes and more girls in the richer classes; but at best the differences on which these statements rest are small, and other statistics seem to give a contradictory result.

In support of the view that the conditions of nourishment affect the proportion of the sexes, the following data have been appealed to. In France the proportion of male to female births is for the upper classes as 104.5 to 100, and for the lower classes as 115 to 100. In the Almanach of Gotha there are recorded 105 males to 100 females; but amongst Russian peasants there

are 114 male births to 100 female births. The statistics for the nobility of Sweden show 98 male births to 100 females, while for the clergy of the same country 108.6 male to 100 female births.

Düsing, in particular, has developed this point of view. It is not evident, however, that because more food is supplied, the individual is necessarily better nourished, for this will depend on other conditions as well. The amount of food taken, or accessible, does not necessarily mean that more is digested.

It has also been pointed out in man that when twins develop, each gets less nourishment than when only a single embryo is present. The smaller size of twins shows that less food is available, yet the proportion of male and female twins is the same as that for single births.

Punnett has examined some statistics based on the census of London for 1901. He finds more females born in the poorest classes, and more males in the highest classes. Intermediate classes give intermediate results, *i.e.* more nearly an equal proportion. Even after taking into account the differential birth rate, the results are still the same; for this and other factors diminish the proportion of males in the poorer classes and make even more probable the conclusion that more males are born under favorable conditions. Punnett draws the conclusion that the determination of sex is independent of parental nutrition.

If nutrition were in reality a factor of any importance in sex determination, it is surprising to find so little difference under apparently very favorable and unfavorable conditions. It seems much more probable that if the nutrition affects in any way the proportion of the sexes, it does so indirectly by elimination, and not by determining either the sex of the embryo or of the egg.

This conclusion is borne out by the results of some experiments on other mammals recently carried out by Cuénot and by Schultze.

Cuénot reared two sets of albino rats: one set was well fed with a variety of food; the other set was poorly nourished, being fed mainly on bread. The well-nourished individuals produced

more young in a litter than the poorly nourished. Putting together all those cases where more than nine young were present in a litter, which indicates favorable parental conditions, there were produced 49 females and 43 males. Where fewer than 9 were born there were 62 females and 71 males. Although there is a slight excess of females in the former and of males in the latter cases, the numbers are so nearly equal that the influence of nutrition cannot be said to be apparent. It may be noted that when more young are present the conditions for each are poorer, yet, in fact, more females were born.

Schultze has carried out some experiments with white mice. One lot was starved. They were long in reaching maturity, and weighed only a half to a third as much as well-fed mice. This lot produced 4 males and 4 females. Another lot produced 42 males and 48 females. Clearly there was no effect of nourishment to be seen. Schultze also examined the product of the second generation of starved mice, some of which were also starved and others fed. He obtained 36 males and 43 females for the starved ones, and 20 males and 28 females for the well-fed individuals. He also paired poorly fed males with well-fed females in order to see if, as has been claimed, the better-fed parent would determine the sex. Well-fed females paired with well-nourished males gave 46 males and 36 females. The same females were then paired with poorly nourished males and gave 38 males and 37 females. Again there is no evidence of the sex being determined by the condition of the parent.

Schultze also tried the effects of feeding mice on foods that were rich or poor in albumen. Potatoes and bacon were used as having little albumen, but on this diet the animals did not reach sexual maturity. Fed on white bread and water, they gave 18 males and 22 females. For a food rich in albumen, tropon [1] was used, also other food rich in albumen, along with salt and milk. There were produced 29 males and 26 females.

These experiments go far toward establishing the view that

[1] Tropon contains 21 per cent albumen, 60 per cent carbohydrates, and 15 per cent fat.

the sex of the egg or embryo of mammals is not determined by nutrition.

Geddes's and Thomson's Theory of Sex

The theory of sex that Geddes and Thomson elaborated in their book on "The Evolution of Sex" is largely based on evidence of the sort just examined. We have seen that all of the earlier experiments that seemed to show that the sex of the embryo is determined by the amount of food supplied are open to grave suspicion. Hence the strongest evidence brought forward by Geddes and Thomson in favor of their theory is no longer valid; but since the theory is also based on certain supposed analogies between the male and female condition in general, we may briefly consider it here.

Geddes and Thomson think that the greater activity or "vitality" of the male is due to a greater breaking down or katabolism of the tissues; while the less active female condition is more one of building up, or of anabolism. "Deficient or abnormal food, high temperature, deficient light or moisture, and the like are such as tend to induce a preponderance of waste over repair — a relatively katabolic habit of the body — and these conditions tend to result in the production of males. Similarly the opposite set of factors, such as abundant and rich nutrition, abundant light and moisture, favor constructive processes, *i.e.* make for a relative anabolic habit, and these conditions tend to result in the production of females." It is pointed out that the males themselves are often smaller, more active, have a higher temperature and a shorter life; while the females are larger, more passive, vegetative, and conservative forms. The authors handle the entire problem of sex under the quasi-symbolic terms of anabolism and katabolism without stating definitely how such a condition determines sex. In fact, so vague and general are most of the statements regarding sex determination that their interpretation belongs rather to that class of hypothesis, so common in much of our biological speculation, in which the issue is obscured by the appeal to phenomena as uncertain

and little understood as the problems that they pretend to explain. If we inquire whether the greater katabolism or anabolism of the male causes it to develop male or female producing spermatozoa, we shall find no definite answer to our question. The idea is, however, expressed that the condition of the mother determines the kind of egg she produces, — male or female, — also that the effects of nutrition in the embryo itself determine its sex, which is assumed to be formed at some early stage in the embryonic or larval development.

If the anabolic state is the one characteristic of the female, how can she be supposed to produce male eggs, for however much starved her tissues may become, she is not thereby changed into a male, and until this occurred it is not clear why male eggs should appear, unless the eggs are supposed to be more easily affected than the formed tissues of the parent. But the most serious objections to the theory are the two following: Statistics show that even under extremes of nourishment of the parent both males and females appear, and if any difference of ratio is found, it is so slight that one can only be surprised that the data give such meager results in favor of the theory. If, on the other hand, the determination of sex is supposed to be due to the nourishment of the embryo, the best-ascertained facts, both experimental and statistical, are diametrically opposed to the hypothesis. The results show rather that differences in nourishment may cause a greater mortality of one sex, or possibly that they favor the development of one kind of egg rather than the other. Therefore unless Geddes and Thomson can give their view, either a clearer interpretation, or bring it into accord with the best-ascertained facts, I do not think it can be looked upon as having in any degree given even a proximate solution of the problem of the determination of sex.

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CHAPTER XXVI

INTERNAL FACTORS OF SEX DETERMINATION

MANY suggestions have been made concerning the internal factors that determine sex. We may roughly classify these views under two headings; namely, those in which the condition of the parents when the germ-cells are liberated is supposed to determine the sex of the individual,[1] and second, those in which some internal change that determines the sex is supposed to take place in the germ-cells themselves irrespective of the condition of the parents. The different hypotheses when brought together seem to include nearly all of the possible conditions that might be imagined to determine the sex of the offspring. We may group the different views under the following headings: (1) the age of the parents; (2) the condition of germ-cells at the time of fertilization; (3) the vigor of the parents; (4) the effects of inbreeding; (5) the size of the egg; (6) the ratio of nucleus to cytoplasm; (7) the extrusion of the polar bodies; (8) the formation of male and female spermatozoa and eggs; (9) the influence of fertilization; (10) the influence of the cytoplasm.

Age of Parents

The only data bearing on this question are those for man and for some of the domesticated animals. Hofacker (1823) and later Sadler (1830) brought together some statistics that seem to show that when the father is older than the mother more boys are born; and when the mother is older than the father

[1] This influence, being in part external to the germ-cells themselves, might be classified as an external influence in the same sense that food is an external factor. There is no sharp line to be drawn in such cases between internal and external factors.

more girls are born. Other writers have published statistics that give exactly contrary results. Geddes and Thomson give such data in the following table: —

Observer	No. of Births	Locality	Father Older Propt. Males to 100 Females	Father Same Age as Mother	Father Younger than Mother Propt. Males to 100 Females	Average Proportion of Males to 100 Females
Hofacker	1,996	Tübingen	117.80	92.00	90.60	107.50
Sadler	2,068	England	121.40	94.80	86.50	114.70
Göhlert	4,584	———	108.02	93.30	82.60	105.30
Legoyt	52,311	Paris	104.49	102.14	97.50	102.97
Boulanger	6,006	Calais	109.98	107.92	101.63	107.90
Noivot	4,000	Dijon	99.70	———	116.00	103.50
Breslau	8,084	Zurich	103.90	103.10	117.60	106.60
Stieda	100,590	Alsace-Lorraine	105.03	———	108.39	106.27
Berner	267,946	Sweden	104.61	106.23	107.45	106.00

It will be seen that while three other statisticians obtained the same kind of results as did Hofacker and Sadler, two others give exactly opposite results. Contradictory evidence has also been given for horses and sheep. As Schultze points out, the results may mean, if they mean anything, that the conditions do not determine the production of one sex or the other, but the survival of an excess of one or the other kind of egg. Bidder has shown in the case of women under 18 years of age bearing children that there is an excess of boys in the proportion of 133.9 boys to 100 girls.

Schultze tried to test this problem experimentally. Sexually immature female mice were placed with males of the same age, so that at the first period of heat conception might occur. The females at this time were between 10 and 15 weeks old. There were produced in all 60 males and 65 females. In other cases the females were isolated and first allowed to breed after the

10th, 12th, 14th, 15th, 16th, 21st, and 28th weeks. In none of these cases was there found any evidence in favor of the view that the sex of the first-born young is affected by the age of the parent.

Condition of the Germ-cells

It has been claimed in the case of certain mammals (Thury, 1863, Düsing, 1838) that if the egg is fertilized soon after leaving the ovary it *tends* to produce a female; if not fertilized till later, it tends to produce a male. Thury based his conclusions on 29 experiments with cows, in which union took place at the beginning or at the end of the period of heat. Others have failed to confirm his conclusions, and contradictory results have been obtained with rabbits and hens. The same argument has been applied to the condition of the sperm, but there is no clear evidence in its favor. It has been pointed out that such a view is contradicted in the case of bats, in which the spermatozoa, received by the females, may remain alive for months before the eggs are set free; and yet the same proportion of males and females found in other animals are produced. In the case of the bee the sperm is stored up in the seminal receptacle of the queen for several years; yet in all cases the fertilized eggs produce only females.

Vigor of the Parents

Schultze has carried out an experiment that goes to show that continued or strained reproduction on the part of the female does not affect the proportion of males and females. As soon as the young mice were born they were removed and the mother again produced a new litter. One female produced in a year and 52 days 14 litters, containing 52 males and 53 females. Another female produced in 11 months 12 litters, containing 42 males and 34 females. A third produced in $3\frac{1}{4}$ months 6 litters, containing 20 males and 11 females. A fourth produced in $4\frac{2}{3}$ months 5 litters, containing 19 males and 22 females. The total is 133 males and 120 females, which for the numbers involved is a fair approximation to equality.

Effects of Inbreeding

It is a widespread belief that deterioration in strength or fertility or in both follows close inbreeding, and while there is some evidence to the contrary in many species, still, in a few, the evidence that we have at present indicates injurious effects. Such weakening influence has been supposed to affect the determination of sex. Schultze has carried out a series of experiments to test this view by closely inbreeding white mice. His results show that while for a limited number of births one or the other sex may predominate, yet the general averages show approximately an equality.

Size of the Egg

In three species belonging to widely different groups it has been discovered that the size of the egg is correlated in some way with sex. In Phylloxera the large eggs develop without fertilization into females, and the small eggs into males. In Hydatina senta the same rule holds. In Dinophilus apatris, also, there are large and small eggs, both of which are supposed to be fertilized. The large eggs produce females and the small ones males. One of the most striking instances in which sex seemed to be determined by, or connected with, the size of the egg is that of the silkworm. Joseph, in 1871, and Mme. Brocadello, in 1896, stated that the large eggs became females and the small ones males. As the following table shows, the small eggs gave from 88 to 95 per cent of males and the large eggs 82 to 92 per cent of females: —

BROCADELLO'S TABLE FOR THE SILKWORM MOTH

Race	Per Cent of Males (Small eggs)	Per Cent of Females (Large eggs)
Vartansi dihhorassan	88	82
Giallo Perugia	95	92
Chiacian di Chorassan	90	92
Giallo Pirenei	88	92
Giapponese verde	88	88
	89.8	90.6

Unfortunately for this case a reëxamination of the problem by Cuénot has lead to a contradictory result. Cuénot separated the large eggs from the small ones by passing them through the meshes of sieves of different sizes. The results appear in the next table:—

CUÉNOT'S TABLE FOR BOMBYX MORI

	Small Eggs		Large Eggs	
	Male	Female	Male	Female
1 set	23	16	79	82
2 set	43	36	31	26
3 set	46	53	9	9
4 set	24	24	6	15
	138	129	125	132

There were no deaths in this set. It will be noticed that there is a slight excess of males for the small eggs and of females for the large eggs, which is in accord with Brocadello's hypothesis, but the difference is too small perhaps to warrant one in concluding that there is a definite relation between the size of the egg and the sex of the moth.

In another experiment, in which, however, there were some deaths, the small eggs produced 119 males and 133 females, and the large eggs 65 males and 108 females.

Cuénot also found in the moth Ocneria dispar that one lot of large eggs gave 14 males and 18 females. These results lend, however, little or no support to Brocadello's view. Wherein the difference in the results lies is difficult to explain. It is hardly possible that Brocadello's results can be accidental or erroneous. Possibly the difference may lie in the fact that in the one case the largest and smallest eggs laid by different individuals were compared, and in the other case the largest and the smallest eggs of the same batch were compared. If the eggs laid by different individuals differ in size, it is possible that the same difference may extend both to male and to female eggs, hence accurate results could only be hoped for by comparing the eggs of the

same batch. In any case it is not clear, even if large eggs produce fewer males and small eggs more males, whether the result is due simply to the size determining the sex, or whether the female eggs tend to become larger than the male eggs. If analogy has any value in this instance, it seems more probable, from the cases of Phylloxera, Dinophilus, and Hydatina, that sex may be sometimes predetermined in the egg and this determines its size. The question needs, however, a reëxamination.

Ratio of Nucleus to Cytoplasm

In a recent contribution Richard Hertwig has argued that sex is determined by the relation of nuclear size to cell size. He bases his argument on a supposed analogy with certain conditions found in the protozoans, and on some experiments of his own and of his pupils on Dinophilus, Daphnia, and Frogs. The experiments on Daphnia have been already given. Hertwig thinks that after a succession of parthenogenetic generations the nucleus in the egg-cell slowly increases — to judge by analogy with the protozoa — and this leads toward the production of males. This tendency may be held in check by a high temperature, but if the temperature is lowered, males appear. The argument is clearly based on a highly hypothetical comparison, and lacks direct observation in its support. Issakowitsch's experiments seem to show that lack of food and not temperature determines the turning point in the life-cycle of Daphnia.

Hertwig's experiments with frogs are very inconclusive, and so far as they go lend little or no support in favor of his view. Eggs of Rana esculenta, that had been forced to premature ripening, fertilized by a male already at its full sexual ripeness, gave the following results. Of 40 individuals that reached the frog stage, all were males. There was, however, a high rate of mortality, and the results may only mean that all the females died. In another experiment some eggs were fertilized at once, others after 8 hours. The latter Hertwig thinks must have been

"overripe." Only a small number of them segmented. The next table gives the results: —

Normally laid eggs, Culture B	90 females	78 males
Normally laid eggs, Culture C	21 females	89 males
Normally laid eggs, Culture D	84 females	189 males
Overripe egg, Culture E	13 females	317 males

The excess of males is much greater in the overripe set. Hertwig concludes from these data that the overripe condition favors male production, because the nucleus undergoes an increase in size during the period of overripening. The improbability of this assumption is manifest when we recall that when the eggs have reached the uterus, the nucleus has disappeared as such, and the second polar spindle has formed in the egg. In regard to the results from the eggs prematurely fertilized, Hertwig thinks that they can be accounted for by assuming that the cytoplasm has not fully developed at this time; but this assumption also seems improbable, since the eggs of the frog reach their full growth in the autumn of the year preceding their deposition. Hertwig's attempt to bring these results — as well as others relating to the influence of temperature as a sex-determining factor in the frog's egg — seems forced, and his general theory finds little support, I think, in the outcome of his experiments.

The Extrusion of the Polar Bodies, and the Analogous Process in the Sperm-cells

The fact that the egg throws off two polar bodies before it begins its development has led to much ingenious speculation in modern times. Amongst other views that have been suggested as to the meaning of this "maturation" process it has been urged that in one or both of the polar bodies the male or the female element is ejected. This view was first proposed by Minot in 1877, and adopted later by Balfour, 1879, and by van Beneden, 1883. More recently Castle has offered a more elaborate hypothesis that rests on the same foundation.

The discovery that most eggs extrude two polar bodies was

followed much later by the discovery that a process similar to the formation of the polar bodies takes place in the male germ-cells. This seemed to be in contradiction to the hypothesis that the elements of the one or of the other sex are ejected from the egg, but the difficulty has not been found theoretically insuperable. An examination of what takes place during the "maturation divisions" of the egg and the sperm-cell will make this clearer.

When the egg nucleus breaks down, preparatory to the formation of the first polar body (Fig. 25, 3), it is found that the chromosomes are only half as many as were present in the earlier or oögonial divisions of the same germ-cells (Figs. 1 and 2). It is generally admitted that this reduction in number is due to the chromosomes having united in pairs. It is also supposed that, during this pairing of the chromosomes, one derived from the male parent (the paternal chromosome) unites with its homologous maternal chromosome. In cases where the chromosomes are of very unequal sizes, there are, with rare exceptions, two of each kind in the early germ-cells, one derived from each parent, and those of the same size are supposed, as stated, to pair with each other (Fig. 3). Therefore when the polar spindle is formed, the chromosomes, half in number, really represent double chromosomes. These chromosomes separate again when the first polar body is given off, half going to one pole and half to the other pole of the spindle (Fig. 4), so that some of the chromosomes in the first polar body are maternal and the others paternal chromosomes. If all of the paternal chromosomes were turned toward one pole of the spindle, and all of the maternal toward the other pole, there would be a complete separation of the chromosomes derived from the mother from those derived from the father. But for certain theoretical reasons it is supposed that this does not take place, but that there is generally a haphazard separation leading to a mixture of maternal and paternal chromosomes at each pole, although one of each kind is present at each pole.

The chromosomes that remain in the egg become quickly arranged on a new spindle (Fig. 5). Each then splits lengthwise, as in ordinary cell divisions, and a half of each goes to one

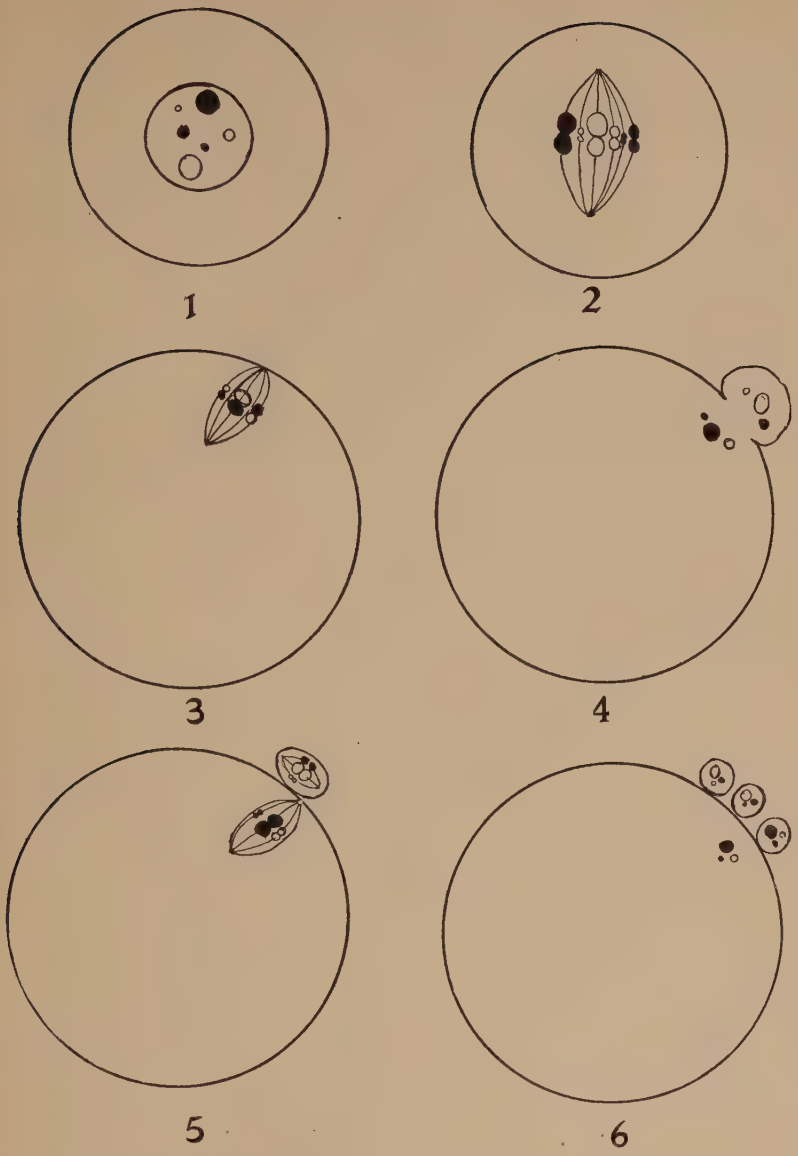

Fig. 25.—Diagram to show formation of polar bodies in egg: 1, early germ-cell, oögonium, with whole number of chromosomes — paternal, black dots; maternal, clear rings; 2, division of oögonial cell; 3, first polar spindle; 4, first polar body; 5, second polar spindle and division of second polar body; 6, egg after extension of polar bodies.

pole and the other half to the other pole, and the second polar body is formed (Fig. 6). Thus while the first division is a *differential* division, the second is an *equation* division. It is supposed, also, that in some eggs the above order is reversed, and the first division is an equation division, and the second a differential one. The end result is the same in both cases.

An exactly parallel series of events takes place in the formation of the spermatozoön. The early sperm-cells, the spermatogonia, contain the full number of chromosomes. These pair, as in the egg, and two cell divisions take place later, — one a differential, and the other an equation division. In the case of the sperm-cells, however, all four cells become functional spermatozoa, while in the egg the polar bodies do not develop. The first polar body often divides. The three polar bodies and the egg are equivalent to the four spermatozoa.

What support do these results give to the hypothesis that sex is determined at one or at both of these divisions? The facts so far stated furnish no real support for this idea, since the differential division merely separates a paternal from a maternal chromosome; and if we do not confuse paternal with male producing, and maternal with female producing, there is nothing in the facts, as I have said, that supports the idea that this division is a sex-determining one. In regard to the equation division, the observations show that the chromosomes split into exactly like halves, and there is also nothing here to support the idea that one half is male and the other half female determining, for this division resembles, outwardly at least, all other equation divisions of the body-cells that are supposed to produce equivalent parts.

If this were the only evidence we possessed in regard to the maturation divisions, it would lend no support to the hypothesis that the sex of the egg or of the sperm is determined at this time; but there are some recent observations showing that in a few groups two kinds of spermatozoa are formed, so far as their chromosomal contents is concerned, and we must now examine

the evidence to see whether, in these cases, sex is determined by the kind of division that takes place in the sperm.

The Formation of Male and Female Producing Spermatozoa

It has been known since 1836 that two kinds of spermatozoa[1] are present in the snail Paludina, and both kinds have been found in the upper part of the oviduct where the egg is fertilized, but whether both kinds are functional is not known. Meves has studied recently the method of formation of these two kinds of spermatozoa. The hair-like spermatozoa resemble the ordinary forms of spermatozoa, the worm-like spermatozoa have a long, rounded, worm-like shape, as the name implies. In the formation of the worm-like form, a peculiar and perhaps a degenerate process occurs. Instead of containing the reduced number (seven) of chromosomes, it gets only a single chromosome.

Two kinds of spermatozoa are also described by Meves in the butterfly Pygæra. One of the two kinds contains no chromatin material whatever. It is headless and perhaps functionless also.

In addition to these cases giant spermatozoa, double the size of the normal ones, have been described in several groups, especially in amphibians and birds. They are due to the incompleteness of one or of both of the spermatocyte divisions, and may be only abnormal forms incapable of fertilizing the egg.

The most remarkable spermatozoa, however, are those in which half of the spermatozoa contain one more chromosome than the other half.

Henking discovered in 1890 the presence of a peculiar chromatin-like body in the spermatogenesis of the bug Pyrrhocoris. It has since been shown that this body is a true chromosome, although it behaves differently from the other chromosomes in certain respects. The more recent work of McClung, Montgomery, Paulmeier, Sutton, Stevens, and especially of Wilson, has cleared up some of the most important questions connected with the behavior of the accessory chromosome.

[1] Discovered by von Siebold.

During the early divisions of the sperm-cells, the accessory chromosome behaves like an ordinary chromosome, *i.e.* it divides into equal parts at each division. But in the two final divisions of the male cells, — the spermatocyte divisions, — the accessory chromosome shows certain peculiarities. It can sometimes be distinguished from the other chromosomes by its slightly different affinity for stains, by its inertness in one of the divisions, by its forming at times a separate vesicle, and especially by the fact that at one of the spermatocyte divisions it fails to divide when the other chromosomes divide. It passes bodily to one pole of the spindle; hence only half of the spermatozoa contain the accessory.

It has been shown by Wilson with great probability that the failure of the accessory to divide, when the others do so, is due to the fact that it has no mate, as have all the other chromosomes, so that when the other pairs separate the accessory remains single. It has been suggested by other observers that the accessory is a double chromosome, like the other pairs, but that it fails to separate into its components when the others so separate. This view seems improbable, because Wilson has found a continuous series of species in some of which the accessory has a partner of equal or of slightly smaller size, while in others the difference in size is very unequal — one being almost a vanishing chromosome. We can imagine that one step farther would lead to the complete disappearance of the mate of the accessory, so that it would have no pair. Whether the disappearance is really due to its vanishing away, or to the absorption by its mate, we cannot even surmise with any degree of probability. If the latter view should prove correct, the accessory is a double or fused chromosome, but not formed by temporary union as are the others at one time, but by a permanent fusion.

McClung offered the suggestion that the difference between the two kinds of spermatozoa, with and without the accessory, is connected with sex determination. His argument was that since there are two kinds of sexual individuals, and two kinds

of spermatozoa, presumably both functional, there may be a connection between the two conditions. This tacitly assumes that all of the eggs are alike, which was apparently taken for granted by McClung, but not examined. Since the accessory is found in one half of the spermatozoa, McClung conjectured that those spermatozoa that contained the accessory produce males, presumably because of the seeming necessity for the new males to have an additional chromosome, the accessory. This argument proved invalid in the light of the observation of Wilson, that the female and not the male contains an additional chromosome, and of Stevens that the female of Tenebrio molitor contains the large chromosome (the homologue of the accessory) and the male the small chromosome.

In order to show how this process works itself out, let us take the case of Anasa tristis, in which there are 21 chromosomes in the male somatic cells and 22 in the female. There will be 11 chromosomes in half of the spermatozoa and 10 in the other half. All of the eggs may be supposed to contain 11 chromosomes. When a 10-chromosome spermatozoön fertilizes an egg, there is formed a male with 21 chromosomes, whose sperm will again contain 10 and 11 chromosomes; when an 11-chromosome spermatozoön fertilizes an egg, there will be 22 chromosomes — the new individual will contain 22, and its eggs will later all contain 11 chromosomes. The accompanying scheme shows this result graphically: —

Spermatozoön		Egg		Male		Germ-cells
10	→	11	=	21	→	10 or 11
or		or		Female		
11	→	11	=	22	→	11 or 11

The evidence that the eggs are all alike and contain the larger number (*i.e.* 11 in the case just cited) is indirect, but apparently conclusive. The chromosomes of the polar spindles have not been counted, but the somatic cells contain 24 chromosomes, as well as the early germ-cells before the pairing of the chromosomes. Moreover, in those cases in which the accessory of the

male can be identified by its size, two such chromosomes have been shown by Wilson to exist in the egg.

In these cases we have conclusive evidence that sex is associated with certain kinds of spermatozoa. Two important considerations arise: first, in what way does this take place; and second, can we extend the same conclusion to other forms? Let us examine in turn these two questions.

How does the spermatozoön with the accessory produce the female? Two possibilities immediately suggest themselves,—either the accessory chromosome contains the elementary characters of the female sex, or it produces its results quantitatively. The former alternative rests on the assumption that the chromosomes contain the unit-characters of the germ-cells. It is this view of the chromosomes that in general meets with wide favor at the present time. Historically it goes back to the gemmule hypothesis of Darwin, the pangenes of de Vries, the biophors of Weismann, etc. — not to give other examples. Those who believe that the characters of the species are contained in living units of the germ that reside in the chromosomes, and wander outward into the cell to bring about the cytoplasmic differentiation, will probably accept this first alternative in regard to the influence of the accessory; but those who find this view improbable will be more inclined to the alternative view.

There is one objection to the idea that the accessory carries the female pangenes, that Wilson has pointed out, and which may be a serious difficulty for this view. If we follow the history of the accessory, we find that it passes from the female-producing sperm into the egg to form there one of the pair of chromosomes homologous with the accessory. In the next generation the homologous chromosomes in the egg are supposed to separate again, one going into the polar body and one remaining in the egg. Now on the theory of chance, either one of the pair might remain in the egg, and should it happen to be the "male-determining" chromosome, the egg should give rise to a male if entered by a male-determining sperm; but if entered by a female-determining sperm (*i.e.* with the accessory), the two chromosomes

would have exactly opposing influences. Apparently the only way out of the dilemma is to assume selective fertilization on the part of the sperm, so that only male-determining spermatozoa (*i.e.* those without the accessory) can enter eggs containing the male chromosome, and only female-determining (*i.e.* those with the accessory) can enter eggs containing the female chromosome. Thus the primary assumption forces us to make another one that lacks at present evidence in its support. Moreover, instead of offering us a simple explanation of sex-determination, the hypothesis seems unnecessarily complex, since it postulates that both eggs and sperm are male or female producing, while theoretically the result could be as readily accomplished by one of them only being male or female producing.

The complication is primarily due to the assumption that the accessory chromosome is a carrier of female pangenes or biophors. If we reject this assumption, we find, I think, a simpler explanation of the influence of the spermatozoön carrying the accessory in determining sex. Suppose we assume that the result is due to the greater amount of chromatin brought into the egg by the sperm with the accessory. It will make no difference on this assumption which one of the homologous accessory chromosomes happens to be present in the egg. The result is parallel to that of the bee, in the sense that the fertilized egg contains more chromosomes than the unfertilized, and produces in consequence the female. In the absence of all knowledge as to how the greater quantity of chromatin produces a female, one is tempted to assume that the result is reached through assimilative changes that take place in the early cells, and there is some evidence in favor of the view that one of the main functions of the chromatin is to carry on the assimilative processes in the cells.

The egg of the bee if fertilized produces a female, if unfertilized a male. This relation has led a number of zoölogists to conclude that all the eggs are male, but become female on fertilization, since the female element introduced by the sperm dominates the male elements of the egg. The spermatozoa con-

tain from this point of view the female elements. The conclusion seems plausible, if we believe that the male and female elements as such become separated in the spermatozoa and eggs. It seems to me, however, that a simpler hypothesis may be formulated. The sex of the embryo is not laid down as such in the egg or sperm, but may be determined later by the quantitative relation resulting from the activity of the chromatin in the cells of the embryo: not in the sense in which Richard Hertwig has expressed this relation, viz. as depending on the size of the nucleus, but rather as the result of the increase in the assimilative function of cells containing more chromatin material. On the other hand, if the number of chromosomes in the unfertilized egg of the bee become doubled before segmentation, the fertilized and unfertilized egg will both produce cells having the same number of chromosomes, and it is difficult to see how a purely quantitative difference exists. It remains, however, to be shown what really takes place in the drone eggs.

Since all intermediate stages have been found by Wilson and by Stevens between cases where the accessory is single and where it has a partner of unequal or of equal size, it may seem probable that even when we cannot recognize it by its singleness or by its size difference, it is still a sex determinant. This argument would be valid if it could be established that unit-characters are carried by individual chromosomes; but if the influence of the chromatin as a sex determinant is purely quantitative, the argument based on a continuous series loses its force; for as soon as the difference in size ceases, the quantitative factor disappears. However this may be, the importance of the discovery of the accessory in sex determination should not be minimized; for it is the one clear case in which an internal factor has been found that is associated with sex production.[1]

LITERATURE, CHAPTER XXVI

(See Chapter XXVII.)

[1] The case of the bee and the ant that have long been known furnish another and perhaps a parallel case.

CHAPTER XXVII

THE INTERNAL FACTORS OF SEX DETERMINATION (*Continued*)

The Origin of Gynandromorphs

THERE are occasionally found, especially in certain groups of insects, individuals that have the characters of the male on one side of the body and of the female on the other. Such cases occur most often in bees, ants, and butterflies; and since in the first, at least, it has been shown that the female sex is determined by fertilization, and the male by the lack of fertilization, it seems probable that when both sexes appear in the same individual that this may be brought into connection with the fertilization. These mixed sexual individuals are known as gynandromorphs. The most celebrated case of this sort is that of the Eugster hive of honey bees, studied by von Siebold. Similar instances had been seen before, but von Siebold studied the forms more thoroughly, and brought his results into connection with Dzierzon's theory in regard to sex determination in bees.

The hive in which these gynandromorphous bees occurred contained an Italian queen bee and German drones. The workers that were produced were therefore hybrids. It is not known whether the hybrid character of the workers had anything to do with the frequent occurrence of gynandromorphism amongst them. Purely bred colonies have also produced these abnormal forms. The gynandromorphs showed the male characters sometimes on the right side of the body and the female characters on the left, or *vice versa;* sometimes the anterior end was male and the posterior female. Sometimes the male and female character occurred in different parts of the same organ, as in an eye or in an antenna. The normal worker

has a sting, the drones are without this organ. When the abdomen of the gynandromorph was like that of a worker, the sting was perfectly developed; but if the abdomen was more or less like that of a drone, the sting was deformed and soft; and when the abdomen was entirely male in character, the complicated capulatory organs resembled completely those of a normal drone, and the sting was absent.

In regard to the internal reproductive organs, great irregularity was found to exist. No definite relation was observable between the kind of the somatic part and its contained reproductive organ. Male and female parts were often combined in the reproductive organs themselves, ovarian and sperm chambers being united in the same organ. In a few cases, where externally a normal male genital apparatus was present, ovaries and oviducts occurred.

Von Siebold thought that these results could be explained in accordance with the Dzierzon theory on the grounds that an insufficient number of spermatozoa entered the egg so that parts of it lacked sufficient quantities of the male element. This view is, in principle, the same that has been used in more recent times to explain the same result; although, owing to our completer knowledge of what takes place in fertilization, we can bring the interpretation into better accord with modern views.

Gynandromorphs have also been found in other groups of Hymenoptera. There are some eighty cases recorded by Dalle Torre and Friese in 1899. Wheeler has recently reviewed all previously recorded cases in ants and described some new ones. In the group of butterflies and moths as many as 1074 cases are recorded by O. Schultz.

Boveri has offered the following theory to account for the appearance of gynandromorphous forms. He assumes that the spermatozoön fails to unite with the nucleus of the egg, but after the female nucleus has divided, the male nucleus conjugates with one of the two resulting nuclei. Consequently there will be present in the embryo two kinds of nuclei, — one kind derived from the single nucleus resulting from the first division, and the

other kind resulting from the united nuclei. The former should produce only male parts, because this is what happens when the egg is not fertilized; the latter should produce female parts, as does a fertilized egg. In other words, the results in the different parts of the single, imperfectly fertilized egg are the same as those formed in unfertilized and fertilized eggs.

I have pointed out that the results are capable of being equally well explained in another way. It has frequently been noted that two spermatozoa occasionally enter the egg of the bee. If we suppose one of these only conjugates with the female nucleus, its products should produce female parts, while the other sperm nucleus that fails to conjugate will, if it divides and produces nuclei, give rise to male parts. Boveri's view and my own are not mutually exclusive: either process may at times take place and produce gynandromorphs. I have pointed out how it might be possible under certain conditions to determine whether the one or the other process has taken place. In a case like that described by von Siebold, in which the mother belongs to one race and the father to another, the parts of the embryo that contain the single nucleus should be like the mother on Boveri's view, and like the father on my own; in both, the parts supplied by the conjugated nuclei produce a hybrid result. An example may make this clearer. Let us suppose, as in von Siebold's case, that the queen is Italian and the male a German drone. If one spermatozoön enters the egg and conjugates with one of the first two segmentation nuclei, as on Boveri's view, the male parts of the embryo that come from the single segmentation nucleus must be like the mother, *i.e.* they should have the character of the Italian bees; the parts that come from the conjugating nuclei should be hybrid. On my view two spermatozoa enter the egg, one only conjugating with the egg nucleus. The male parts will come from the single sperm nucleus, and will, therefore, be like the father, *i.e.* they will have the character of the German bees; the parts that come from the conjugating nuclei will be hybrid in character. Thus on my view the male parts of the gynandromorphous hybrid will be paternal; on Boveri's

view, they will be maternal. At present we lack the data to decide between these alternatives.

In other groups of animals, gynandromorphous forms are great rarities. Weber described a finch that had feathers like the female on the left side and like the male on the right. There was also an ovary on the left side and a testis on the right. Until we know more of the conditions that determine the sex of birds, it is useless to speculate about this case.

The Sex of Multiple Embryos

Another group of facts discovered in other hymenoptera seems to show that the sex of the embryo is already determined in the egg. The chalcid fly (Ageniaspis fuscicollis) lays its eggs in the egg of a moth. Both eggs develop, the latter into a caterpillar and the former into its parasite. The parasite develops in a most remarkable manner. Marchal (1904) found that from a single egg a chain of embryos develops, and these embryos are all of one sex. Bugnion had already (1891) observed that the individuals that emerge from a single caterpillar are generally of one sex, and both authors have interpreted the result to mean that if the egg has been fertilized, a chain of female individuals is formed; but if the egg is not fertilized, males are produced. More recently Silvestri has studied the early development of another insect (Litomastix truncatellus), and finds, in fact, evidence showing that the eggs may or may not be fertilized, and that it continues to develop in either case. Silvestri finds that a single egg may produce a thousand sexual individuals, and also several hundred sexless larvæ that lack the circulatory and respiratory system. The details of the early development of these forms are remarkable, but cannot be considered at present. The point of especial importance is the conclusion that the sex of the embryo must be determined at an early stage, and is not later altered, since all the sexual embryos of a chain are of the same sex.

It is true that there may sometimes emerge from a caterpillar both males and females, but this is supposed to be due to two eggs —one fertilized, the other not—having been laid in the same egg

of the moth. Silvestri has seen the same egg pierced more than once by the same fly, and we may readily suppose that two individuals often deposit their eggs in the same egg of the moth.

A closely similar mode of development occurs in another species, Polynotus minutus, which deposits its eggs in the larva of Cecidomia destructor, the Hessian fly. Marchal found in fourteen cases that the flies that emerge from the grub are all of one or of the other sex, while in two cases there was a mixture of both sexes.

The Sex of Human Twins and Double Monsters

There remains to be considered another class of facts, not dissimilar from the last, that appear, if certain modern assumptions are correct, also to mean that the sex of the embryo is already determined in the fertilized egg, and is not affected by subsequent events. I refer to the case of human twins. It is said that two kinds of twins occur: in one kind the individuals are not more alike than any two children born at different times: these are fraternal twins. They may be of the same sex or different sexes, and not more often of the same sex than of different sexes. They are supposed to arise from two eggs simultaneously set free from the ovary. In the other kind of twins, the two individuals closely resemble each other — so closely, in fact, that they may scarcely be distinguishable apart by their own parents. These "identical" twins are said to be always of the same sex, and it has been suggested that they arise from the same egg that has become separated into two parts at some stage in its development. This view seemed all the more plausible because in the last decade it has been shown experimentally for some other eggs that when the first two cells are separated each gives rise to an entire embryo. This is true for the eggs of sea urchin and starfish, and in the vertebrates for the egg of amphioxus, the salamander, and the fish. We do not know in these cases that the isolated cells would produce individuals of the same sex, nor do we know in man that the cells are really separated; but

putting the different facts together it seemed plausible, as I have said, that identical twins arise in this way.

There is a further fact that supports this hypothesis. Abnormal embryos are sometimes born, composed of two individuals united in various ways.[1] These are the so-called double monsters, and in the cases in which the sexual organs are separate they are always of the same sex.

In the case where there are three offspring at the same birth, triplets, all three may be identical, or two may be identical and the third only fraternal, or they may be all fraternal. The identical twins are of the same sex, and on the hypothesis they come from one egg, while when two only are identical the third may be of the same or of the other sex. There is at least one authentic case in which all three individuals were of the same sex, and when they grew up were closely similar.

Jehring has confirmed a statement made on hearsay by Azara, to the effect that in the armadillo (Tatusa hybrida) of Paraguay the offspring of one birth are all of the same sex. In two pregnant females examined by Jehring all eight young were males. Each embryo had its own aminon, but all were inclosed in a common chorion. The latter fact is supposed to furnish conclusive evidence that the embryos must have arisen from the same egg; but while this is probable, it has not been shown that the chorions of different individuals might not unite into a common envelope. The same reasoning has been applied to the case of identical human twins that are supposed to be always inclosed in a common chorion.

The idea that the two sorts of twins differ in the respects noted above seems to have been noticed by Dareste in 1874, and by Fisher in 1866; but Galton (1891) has especially drawn attention to this difference. Recently Thorndike has disputed the assumption that there is a sharp distinction between identical twins and ordinary or fraternal twins. Thorndike finds as the result of an examination of a large number of cases that there is a perfect gradation between identical and fraternal twins. He

[1] Wilder (1904) has brought together the records of such cases.

finds, moreover, that "identical" twins may be of opposite sexes. He believes, therefore, that the closer resemblance sometimes observed in children born at the same time is due to the similar conditions of the germ-cells of the parent at the time of conception, or to the more nearly similar environment under which the twins are reared. These two conditions he includes in what he calls the "heredity" of the offspring. In general, the term "heredity" has a different meaning to biologists, viz. to express the idea of the inheritance derived from the germ-cells apart from the special environment to which they or the offspring that they produce have been subjected. Disregarding, however, this difference of definition, the facts recorded by Thorndike cast serious doubts on the assumption that there is a sharp distinction between the two kinds of twins. If the conclusion is substantiated, we have little evidence left on which to base the assumption that identical twins owe their resemblance and their sex to a common origin. If then, as seems probable, identical twins, double monsters, and the like are more often of the same sex, it would appear that special external conditions existing at the time in one or in both parents determine the sex of the embryo. Improbable as this may seem, a careful reëxamination of the evidence should be made.

Two Recent Theories of Sex Determination based on the Assumption of Male and Female Eggs

Beard has proposed an hypothesis of sex determination that rests on the assumption of male and female eggs. He suggests that the sex of the individual is determined by the egg alone. According to his view, the egg and its two polar bodies are of the same sex, male or female. Just as there are two kinds of eggs, there are assumed to be also two kinds of spermatozoa; but these have no function in respect to sex determination, and Beard assumes, in fact, that one kind has even lost its power to fertilize the eggs. When the female egg is fertilized it gives rise to a female, and the male egg to a male. The female produces eggs again of two kinds, male and female eggs; the male two kinds of

sperm, one of them functionless, etc. It is apparent, therefore, that Beard's theory resolves itself into two assumptions: first, that sex is determined by the egg alone; and secondly, that two kinds of eggs are produced. The solution of the problem is merely shifted to a new field, since it is assumed that the male and female eggs are produced, and no explanation of how or when this occurs is forthcoming.

Beard's view encounters, moreover, special difficulties that can only be explained away by further assumptions. For example, in the aphids there is a long succession of female parthenogenetic eggs, ending finally in the production of male and female parthenogenetic eggs. It would seem that external conditions must determine whether the eggs are to be all female eggs or some male and some female, but there is nothing in Beard's theory that indicates how such a thing is possible.

In the case of the bee, Beard is forced into the position of assuming that the sex of the individual is not dependent on whether it is or is not fertilized, although the clearest evidence that we have points unmistakably in that direction. He argues that only female eggs can be fertilized, while male eggs cannot be fertilized; but if this were the case, it is not evident how the queen could distinguish between the two kinds of eggs and lay each in its appropriate cell.

Castle has also proposed a hypothesis of "The Heredity of Sex." His hypothesis is avowedly an attempt to account for the determination of sex by means of the Mendelian method. It had already been suggested by Strasburger and by Bateson that the sexual forms might bear the same relation to each other as do the offspring of Mendelian hybrids. Castle has elaborated this idea into an ingenious hypothesis. He assumes that there are two kinds of spermatozoa, male and female; and two kinds of eggs, male and female. If we assume, as in the case of Mendelian hybrids, that all possible chance combinations occur between the germ-cells, we should expect three kinds of individuals (as in the Mendelian proportion), — males, females, and hermaphrodites. There would be as many

of the latter as of the other two combined, as shown in the formula: —

$$\begin{array}{ll} \text{Spermatozoa} & \text{M} + \text{F} \\ \text{Eggs} & \text{M} + \text{F} \\ \hline & 1\text{MM} + 2\text{MF} + 1\text{FF} \end{array}$$

Since we get no such results in animals, the Mendelian scheme must evidently be altered if it is to be made use of as an hypothesis of sex. Therefore Castle assumes that male spermatozoa can fertilize only female eggs, and that female spermatozoa can fertilize male eggs. Hence every individual is, as it were, a sexual hybrid, since it contains both male and female elements. But what determines the sex of the individual? Castle's hypothesis gives us no answer. It seems to me, therefore, that despite the assumptions of male and female spermatozoa, and of male and female eggs, and the further assumption of selective fertilization, the hypothesis does not advance us toward an explanation of sex determination. If it be claimed that the hypothesis deals only with the heredity of sex rather than with its determination (although Castle places no such limitation on his view), it is still not apparent what the hypothesis accomplishes, since it assumes a separation of the sex-elements (which is entirely hypothetical) only in order to bring them together again by means of selective fertilization (likewise an assumption). Since we have some evidence in favor of the view that both sex elements are carried by the sperm as well as by the egg, the heredity of sex is accounted for without any additional hypotheses.

The Reduction Process in Parthenogenetic Eggs

The question of the number of the polar bodies extruded in parthenogenetic eggs has also played a conspicuous rôle in modern speculation concerning sex determination. Weismann was led by certain theoretical considerations to examine the eggs of parthenogenetic species. He found only one polar body given off in the parthenogenetic eggs of daphnia. This led to the idea that the second polar body may act like the spermatozoön,

and, being retained, brings about self-fertilization. Blochmann showed, however, in the honey bee, that two polar bodies are thrown out from the drone eggs, yet they develop without fertilization. In the rotifer Asplanchna, it has been shown by Erlanger and Lauterborn that while the female parthenogenetic egg gives off only one polar body, the male egg gives off two. These facts show that there is no universal rule in regard to the number of polar bodies that are extruded by parthenogenetic eggs. Furthermore, the fact that in hermaphrodite animals two polar bodies are always extruded also shows that the problem of sex determination is not necessarily connected with this process. It would be erroneous, however, to conclude from these cases that the retention of one polar body may not in certain species be a possible factor in sex determination, although not necessarily because of the retention of male or of female elements.

Since half the inherited chromosomes are supposed to be given off in one or the other polar body, the question arises whether this happens in parthenogenetic eggs in those cases where a single polar body is produced. In the case of the aphids, Stevens has shown that in the division that leads to the formation of the single polar body of the parthenogenetic cycle, the full number of chromosomes is present, and the division of the chromatin is an equation division. There has been no pairing of the chromosomes to give the reduced number, preparatory to the polar body division, as in sexual eggs. Hence the full number of chromosomes is present in the polar spindle. I have obtained the same result in phylloxera; both in the eggs that do not make the sexual forms, and in the male and female producing eggs also. Since the latter produce either male or female individuals, it seems unlikely in these cases, and probably by inference in fertilized eggs also, that the determination of sex is necessarily connected with this division.

At the second or differential division when the other polar body is formed, it is supposed that only the maternal and paternal (united) chromosomes separate. There is nothing, therefore, in this process to suggest that it is connected with sex differentia-

tion. In the case of the unfertilized egg of the bee it has been shown by Petrunkewitsch that the half (reduced) number of chromosomes is left in the egg. He states that there occurs a doubling of the number of chromosomes before the first segmentation nucleus is formed, so that the full number is restored. This result is not in harmony with Meves's study of the spermatogenesis, and as Giglio-Tos has pointed out the whole question is in such a confused state that we must await further observations.

Influence of the Cytoplasm

Most modern theories of sex determination have been based on changes in the nucleus rather than in the cytoplasm. Yet since the differentiation of the cell takes place in the cytoplasm, it may seem that the initial differences might be traced to that part; but owing to the fact that the different parts of the undifferentiated cytoplasm show little differences in staining capacities, it has not been possible to gather many facts that can be utilized in the formation of a cytoplasm theory. One consideration above all others has, I think, led modern cytologists to regard the nucleus rather than the cytoplasm as the initiator in the formation of the characters of the embryo. It has become an unchallenged or seldom questioned dictum that the nucleus must transmit the qualities of the germ-cells, because the qualities of the father are brought into the egg by the spermatozoön, and it is assumed that the nucleus of the spermatozoön is the only part of it that contributes anything worth considering to the fertilized egg. Furthermore, since the nucleus of the spermatozoön consists of almost solid chromatin, it has been inferred that the chromosomes alone carry the hereditary qualities of the germ-cells. But a consideration of all the facts will show, I think, that there is at least a possibility that the protoplasm of the sperm-cell may have something to do with the transmission of the hereditary qualities of the father. If we trace the history of the spermatozoön, we find that at no stage is all of the cytoplasm of the germ-cell from which it arises totally eliminated from the cell. It is true that a part of the cytoplasm — it may be a large

part — is used in the formation of the tail of the spermatozoön, which may or may not enter the egg; but some of the cytoplasm forms at least the centrosome and is carried into the egg. Owing to our inability to follow the history of this cytoplasm in the egg, we have come to ignore its existence, while the nucleus that can be easily traced has occupied exclusively the attention of modern embryologists with rare exceptions.

If we admit that the cytoplasm of the spermatozoön is not only brought into the egg, but slowly increases in quantity there, can we find any clew in such a condition that will help in the solution of the problem of sex determination? There are several possibilities that should be considered. If we suppose that there is predetermined male and female cytoplasm in the egg or the spermatozoön, or in both, we encounter precisely the same difficulties that have been met with by assuming that predetermined elements of these two kinds exist in the nucleus. From this point of view the two assumptions stand on the same footing. If we assume that the determination of sex lies in the cytoplasm, not in the form of predetermined elements male and female, but as one of the alternative conditions of differentiation of the cytoplasm, we must still explain what factors — external or internal — determine whether the one or the other condition shall dominate. Whether this is due at times to a relation between the chromatin and the cytoplasm, or at other times to a relation depending on the condition of nourishment of the cytoplasm, etc., cannot be stated. However probable it might be made to appear that the differentiation that appears in the cytoplasm really *originates* there, and not in the nucleus (except in so far as the latter induces important changes in the cytoplasm through its assimilative changes), the fact remains that we cannot explain the mechanism in the cytoplasm through which the one or the other condition comes to be the dominating one. Here, as in the case of the nucleus, we are too ignorant at present of the real chemical changes that take place to permit of more than purely speculative views.

Ziegler has recently proposed an hypothesis of sex determina-

tion that rests on the assumption that the chromosomes that arise from a female individual have a greater tendency to produce a female; and those that originate from a male individual have a greater tendency to produce a male. Since the child gets as many chromosomes from the father as from the mother, the parental chromosomes as such cannot determine the sex. But it is to be recalled that amongst the parental chromosomes some have come from the grandfather and some from the grandmother. The relative number of chromosomes from the maternal and paternal lines will be variable in number on the current assumption that at the reduction division it is merely a question of chance which member of a pair of homologous chromosomes goes to one pole of the spindle and which to the other. If the chromosomes of the grandfather predominate in the offspring, it will be a male; if the grandmother chromosomes predominate, a female develops.

To take an example. If the somatic number of chromosomes for the human species be assumed to be 24, the child gets 12 from the father and 12 from the mother. If amongst the former there are 8 grandmother chromosomes and amongst the latter 7 grandmother chromosomes, the child will be a girl, for there are at least 15 of the 24 derived from the grandmother's side.

On Ziegler's theory of sex it is evident that whenever the reduced number of chromosomes is even, there may occur an exact balance of grandmother and grandfather chromosomes, hence the child can have no sex at all. In the list of cases given by Ziegler himself, we find that the reduced number of the chromosomes is an even one in 29 species and odd only in 10.

It seems improbable that the equal balance of the maternal and paternal chromosomes could be counterbalanced by the presence of chromosomes derived from the grandparents, especially since these have also been contained in one or the other parent whose sex, on the theory, should have influenced them to acquire the character of that parent. These and other difficulties make Ziegler's hypothesis very improbable.

Conclusions

We have examined the principal data that bear on the problem of sex determination and have found that we still lack the clew that solves the riddle. Nevertheless many important facts that bear directly on this question have been made known, and the ground has been pretty well broken for future investigation. Concerning the various hypotheses that have been proposed, we may place them under two principal headings, which I shall call the morphological and the physiological points of view. Let us examine these in turn.

The Morphological Conception of Sex Determination

According to this view, the characters that stand for the male or the female condition are represented in the germ-cells as pre-existing elements. If we assume that the male characters are eliminated from the egg or spermatozoön, the female characters remaining, the egg produces a female; if the female elements are ejected, the egg becomes a male. This method of treating the problem has the advantage of simplicity, and is capable of diagrammatic treatment. It is the method that has been largely followed by modern theorists. The same principle has been followed in recent years in dealing with the entire problem of heredity. The most serious objections to this procedure are that it is based on an assumption that cannot be verified, and in practice it has not solved, except in a purely formal way, any of the problems of heredity. The problem instead of being solved is merely shifted into an unknown field where the imagination has full sway and where the conclusions cannot be tested.

A modified form of this same method of treatment is to regard heredity as the result of the dominance of one or of the other sex-characters, both unit-characters being assumed to be present in the same egg and sperm. There are certain facts that seem to indicate that this is an advance over the other point of view that regards the germ-cell as either purely male or female; but here

also we lack the clew that tells us in what condition the characters are represented in the egg.

The Physiological Conception of Sex Determination

From this point of view we may consider the protoplasm as a substance capable of assuming one or another condition that is determined, for the time being, by the environment or by internal conditions. We may suppose that the same end-result (sex, for example) may be determined by different factors in different species. I mean that while in certain species one kind of factor commonly determines the result, in other species other factors may determine which of the possible alternatives is followed. The protoplasm may be looked upon as being in a condition of equilibrium as far as the adoption of either alternative is concerned, and which one is followed is determined by those conditions that bring to the front the one or the other possible state.

An illustration may make this clearer. In certain male crabs the right and left chelæ are different in structure. In some species it is always the right-hand claw that is the larger, in others the left, while in some cases either the right or the left is the larger. It has been shown by Przibram for some species of the latter class that if the large chela is removed the small one becomes the larger at the next molt, and in place of the large one removed a small one regenerates in its place. Both claws have potentially the same possibilities of becoming large or small. External or internal conditions determine which kind of development takes place; but the selection once made, the differentiation proceeds strictly along one line.

Now in this case we might assume that when the big claw of one side is removed, all the preformed elements (primoidia) of the big claw contained in all the cells of the small claw begin to develop and dominate and replace the already-controlling-small-claw-forming elements. That is the morphological way of explaining the result. On the other hand, the other — the physiological — idea makes use of no such mechanism, but assumes

that the protoplasm has two possible ways of differentiating which are determined by local conditions, internal or external. The same ways of conceiving the problem may be applied to the case of sex determination.

Which of these alternative interpretations we may think more probable, or more profitable as a working hypothesis, is perhaps, at present, a question of personal choice; for we lack, as I have said, the data to decide between them. For myself, the physiological conception seems more in accordance with our general ideas concerning development, and above all to be a conception that is more stimulating and suggestive as a working hypothesis than the morphological idea, which seems to be quite sterile as a point of view leading to further investigation.

Analysis of the Results

An analysis of the evidence that has been given in the preceding pages concerning sex determination suggests the following considerations.

The average equality of males and females indicates, I think, that external conditions do not regulate the result, but that some internal physiological mechanism exists that determines the sex.[1] This physiological mechanism does not involve the separation of male and female elements or units in the egg and sperm, but only involves the production of those conditions that determine whether one or the other sex will develop. In some cases the initiatory processes may exist in the egg, in others in the sperm, and in still others after the union of egg and sperm. In other words, in all species with separate sexes the potentialities of producing both sexes is present in all eggs and in all sperm; but the development of the one or the other sex is determined by some unknown internal relation. From this point of view it is misleading to speak of male and female eggs or sperm in the sense that such eggs contain only male or female potentialities, for all

[1] Of course this statement does not exclude the possibility that external influences may not determine that the internal mechanism shall become active in one way or another as seen in the cyclical modes of reproduction.

eggs and sperm contain both potentialities, and which is realized is determined by some internal relation that regulates the dominance of one or the other sex.

This idea leads to the following suggestion: — In Mendelian hybrids of the first generation, in which two contrasted characters are present, it is assumed that when the germ-cells are produced half of them show already the dominance of one character and the other half of the other character. This leads, after haphazard matings, necessarily to the three types that appear in the second generation. In the case of sex only two types are produced, hence it is not possible to imagine that two kinds of eggs and two kinds of spermatozoa are produced.[1] It seems, therefore, logical to conclude that the condition that leads to the development of the alternative characters may exist in the egg alone (as for the male bee), or in the sperm alone (as for certain hemiptera), or by the combination of egg and sperm, as for the female bee. In the last case the conditions that will lead to the development of the male are found in the unfertilized eggs; but the addition of the sperm brings in a new condition that leads to the development of the female — not that the spermatozoa of the bee are female or even female-producing, but that the combination of egg and sperm is female-producing. It is conceivable that a non-nucleated egg of the bee fertilized by a sperm would produce a male, the conditions being the same as in the unfertilized egg.

Admitting that all eggs and all sperm carry the material basis that can produce both the male and female, the two conditions being mutually exclusive when development occurs, the immediate problem of sex determination resolves itself into a study of the conditions that in each species regulate the development of one or the other sex. It seems not improbable that this regulation is different in different species, and that, therefore, it is futile to search for any principle of sex determination that is universal for all species with separate sexes; for while the

[1] The assumption of reciprocal fertilization being rejected provisionally for reasons already given.

fundamental internal change that stands for the male or the female condition may be the same in all unisexual forms, the factor that determines which of the alternate states is realized may be very different in different species.

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EXPERIMENTAL STUDY OF SECONDARY SEXUAL CHARACTERS

CHAPTER XXVIII

SECONDARY SEXUAL CHARACTERS

Introduction

HUNTER was the first, I believe, to use the term secondary sexual characters for those differences in structure between the males and females that are not directly connected with the organs of reproduction. One of the most important facts connected with the occurrence of secondary sexual characters is that they are found almost exclusively in the higher groups of animals. Moreover, they are, on the whole, characteristic of certain large groups, so that it might appear that in these groups there is some inherent tendency for such differences to develop. Thus in the groups of mammals, birds, and insects secondary sexual differences are quite common, while in the worms, mollusks, echinoderms, and cœlenterates, the male and the female are closely similar except for the differences in the organs of reproduction. Why the higher and the lower groups should differ in these respects is difficult to explain. Two suggestions have been proposed that may appear to account for the facts. The groups in which these differences are found contain forms that are extremely active, and the males are as a rule more active than the females. Correlated with this difference in activity or "vitality" we may imagine that differences in the development of some of the bodily structures may occur. This is the idea that Wallace has suggested.

The other view is the one proposed by Darwin. He ascribes the differences to the selection by the females of those males that are more highly ornamented, or have finer voices, or that develop certain odors, etc. This selection by the female implies a highly developed condition of the sense organs, and perhaps of

the central nervous system also. We find these organs most perfectly developed in the higher animals, hence it may appear that we can explain on this basis the occurrence of secondary sexual organs in these groups, and the absence of such differences between the sexes in the lower groups with less developed sense organs.

Before we examine critically these and other hypotheses it may be well first to pass in review some examples of secondary characters, and then examine the experimental evidence that shows how far the development of these characters is dependent on the presence of the essential organs of reproduction.[1]

In the mammals there are many excellent examples of differences between the male and the female. In the mandrill the naked skin of the face of the male is bright blue, with the tip and sides of the nose a brilliant red. The face is also marked with white stripes. On the forehead there is a crest of hair and on the chin a yellow beard. In the monkey Cercopithecus diana the head of the male is intensely black, while that of the female is gray. The enormous development of antlers in the stag is a striking example of a secondary sexual difference.

In birds there are many species in which the males are entirely differently colored from the females. The scarlet tanager is a familiar example. The male during the pairing season is a brilliant scarlet, with jet-black wings, while the female is a modest yellow-green. The Baltimore oriole and the orchard orioles show almost as great differences in the coloration of the two sexes. Many of the humming birds show extraordinary differences between the male and female, and the birds of paradise and the peacock excel in this respect.

[1] Darwin brought together in his book on "The Descent of Man" a great number of cases in which secondary sexual differences occur. Wallace also, on several occasions, has given examples of the same sort. Scattered through the systematic literature of the groups of mammals, birds, and insects a vast number of cases are described. Recently Cunningham has also brought together a large number of cases of secondary differences and has suggested another way for accounting for them, as will be stated later. Lameere has also given a number of examples, especially among insects.

Differences exist not only in color and ornamentation, but in other characters also. The male gorilla has a powerful voice, the effect of which is enhanced by the presence of a laryngeal sac. One kind of gibbon can produce a correct octave of musical notes. The vocal organs of the monkey Mycetes are a third larger than those of the female and produce an "overwhelming" sound. In birds also it is generally the male that sings; and in the case of the thrushes and several other groups the voice of the male is highly developed.

The scent glands or odoriferous glands of some of the mammals are also secondary sexual characters. In many cases the glands are present and equally developed in both sexes, but in others the glands become enlarged in the male during the breeding season, while in still other species the glands are more developed in the males or even confined to them. At the rutting season the glands on the sides of the face of the male elephant emit a secretion that has a musky odor. The males of some of the bats have glands and protrudable sacs in various parts of the body. The strong odor of the male goat and of certain deer is well known. In the male of the musk deer there is a region of the tail that is "bedewed with an odoriferous fluid," while in the female this space is covered with hair.

The dances accompanying courtship in certain male birds, and the peculiar antics and apparent displays of plumage shown by these, belong also in the class of secondary sexual differences.

In the group of lizards, amphibians, and fishes, numerous cases of secondary sexual differences are known, and in some of these the differences are almost as marked as in the highest members of the vertebrates.

In the insects many species show secondary sexual differences. In the flies of the genus Elaphomia the males are furnished with horns, recalling those of the stag. They are branched or palmated, and in one species are of a beautiful pink color edged with black. In the butterflies there are many

cases in which both sexes are brilliantly colored, but the number of cases in which the males greatly excel the females is comparatively small. This statement holds also for other groups of insects, where, despite the highly developed coloration, the males are not, in most cases, more ornamented than the females.

In the crustaceans, where highly colored forms are not so common, there are only a few cases of secondary sexual differences, yet in the group of copepods there are some species where the male excels the female in ornamentation even more than does the peacock excel the peahen.

These examples will serve to illustrate some of the more striking differences between the male and the female individuals. Before discussing further the possible interpretations of these facts, let us examine the evidence showing that a correlation exists between the development of the secondary sexual characters and the presence of the essential organs of reproduction.

Correlation between the Secondary Sexual Characters and the Essential Organs of Reproduction

It has been long recognized that in vertebrates there exists an intimate connection between the presence of the essential organs of reproduction and the full development of the secondary sexual characters. The removal of the testes of the male has been sometimes performed artificially, and sometimes has resulted from disease or abnormal development of these organs. The results are well shown in the case of the stag. If very young males are castrated, before the knobs of the antlers have appeared, the antlers never develop. If the operation is performed at the time when the antlers have already begun to develop, complete development does not take place; they remain covered with skin and are not moulted or renewed. They form the so-called peruke antlers. If the stag is castrated when the horns have fully developed, they are precociously thrown off, and are replaced by new antlers, showing a tendency toward peruke-formation, and these are not again renewed. If the castration of the young animal is on one side only, the horns show a

weaker development, but are no better developed on the side opposite to that at which the removal took place than on the same side. The influence, therefore, is a general one, and not one-sided, as has been believed.

If castration in man takes place in youth, it causes several important changes. The growth of hair on the face and other parts of the body is scanty or suppressed. The larynx remains undeveloped, so that the voice retains the high pitch of boyhood. It is also said that the shape of the pelvis is different from that of men, and even that parts of the brain are smaller. The large body size of eunuchs is likewise supposed to be due to the effects of castration.

In oxen and horses, in which castration has been carried out at an early age, the shape of the pelvis is altered, and it is said to approach in form that of the female. It also has been shown, in the case of cattle, horses, rabbits, dogs, and fowls, that one result of castration is to retain to a later stage of development all of the cartilaginous unions between the parts of the bones. This sometimes leads to an increase of growth in length of the bones, especially in those of the extremities, which may account for the immense size of eunuchs. Associated with the increase in the length of the bones is a certain degree of thinness in them.

The statement is often made that the effect of castration of the male is to change his characters into those of the female, and it is not difficult to cite cases that seem to favor this view. The failure of the stag to develop horns reduces him to the condition of the female; the failure of the male fowl to develop the plumage of the cock and the incomplete development of the comb, wattles, and spurs, as well as his inability to crow makes him more like the female bird; the absence of the beard in eunuchs and the retention of the high voice are characters associated with women. These results are so evident that it is not surprising that they have been interpreted as showing that the castrated male has assumed female characters. On the other hand, it has been pointed out that the results can also be interpreted in another way. The castrated male may retain the immature

form and characteristics of the male, and since in the immature condition the male has characters in common with the female, the resemblance may be due to this rather than to the development of the female characters by the male body. For instance, the beard is undeveloped in boyhood and the voice is pitched higher than in man. In these respects the boy resembles the girl, and should he fail to develop a beard and retain his high voice when he is full grown, it may seem that he has assumed the female characters, while in reality he has only retained the immature conditions of his own sex.

There is a further possibility to be considered. Castration may affect changes that are associated with this condition itself and have no relation to the differences between the sexes. These possibilities will show that great caution must be exercised in interpreting the results of castration of the male.

A side light is thrown on the problem from another direction. The removal of the ovaries of the female is supposed to induce the development of male characters, and if this is the case the results would seem to support the converse proposition discussed above. Let us, therefore, next examine this question.

It has been shown experimentally that the removal of the ovaries in young rabbits, guinea pigs, and dogs causes a lack of development of the mammary glands. The uterus also fails to reach its full development. Other effects than these are not recorded. It is improbable that any one will claim that the failure of the mammary gland to develop is due to the assumption of a male character, and yet the argument is not dissimilar from the failure of the larynx to develop in the castrated male, and this has been interpreted, as we have seen, as due to the development of a female character.

There seem to be no cases on record of artificial castration of female deer, but there are a few cases recorded in which the ovaries were degenerate and horns had developed. There are also three other cases, cited by Rörig, in which the young doe showed horns, and it was found upon examination that slight abnormalities were present in the ovaries, but they were so slight

as to make it doubtful if the development of horns was due to this defect. Cases of this sort are not of much value, since it is possible that the abnormalities observed may both be due to some abnormal condition of the whole and are not connected as cause and effect.

The best-known cases in which the castrated female assumes the characters of the male are found in poultry. Many instances of this sort have been recorded.[1] It has also been observed that when female birds, such as pheasants, fowls, partridges, peacocks, and ducks, become old, they may assume the secondary sexual characters of the male. Darwin cites the case of a duck ten years old that assumed the perfect winter and summer plumage of the drake. Waterton gives the case of a hen that had ceased laying and had assumed the plumage, spurs, voice, and disposition of the cock. This evidence points clearly to the possibility of the castrated female assuming the characters of the male. Whether the converse is true for the male is, as we have seen, more doubtful, but the possibility of its being true must be admitted.

If the characters of the female are latent in the male, and those of the male are latent in the female, as these and other facts seem to show, the experiments with castration have an interesting bearing on sex determination; for if, as seems probable, the male characters may develop in a castrated female despite the fact that the female characters had already been developed, it shows that the question of sex determination, even if determined in the egg, or even in the embryo, is not final and the converse change may occur even at a late stage. If it should prove true that in the vertebrates the castrated female develops male characters, but the castrated male does not develop female characters, but simply remains at a lower stage of development, we might perhaps assume that the male condition in this group is a further stage of the female condition. Internal or external factors may determine whether the egg or embryo remains at a given stage or undergoes a further change. If the former, a

[1] Darwin, "Animals and Plants," Chap. XIII.

female develops; if the latter, a male. We lack the evidence to establish such a view at present, and our more immediate problem is first to discover what factors determine the sex of the individual.

So far we have considered only the effects of removal of the essential organs of reproduction, the ovaries and testes, on the general characters. It has been shown for the males that the removal of these organs in youth also affects the accessory parts of the reproductive organs, — the glands and ducts. If the testes are removed from the adult mammal, there is a decrease in the size of the prostate gland that may be due to functional atrophy, or may be due to more direct influences. If the testes are removed from a young animal, the prostate does not develop further, and remains quite small. One-sided castration produces no effect, either on the same or on the opposite side. The development of Cowper's gland seems to be correlated with the development of the prostate, and after castration remains undeveloped. Other parts of the accessory system also fail to develop completely after castration.

It is generally assumed that the influence arising from the testes must be in the nature of an internal secretion, which, setting free certain materials in the blood, affects the development of remote parts of the body. In support of this view is the fact that the influence is not unilateral, but general. There is a further result that shows how important a rôle the internal secretions of the reproductive organs may play in certain changes in other parts of the body. It has been found by Frankel and Cohen that the presence of the cup-shaped corpora lutea, left on the surface of the ovary after the egg has escaped, is necessary for the fixation of the egg to the wall of the uterus. The egg or young embryo fixes itself six days after it has been set free from the ovary. If the ovary is removed at this time, the fixation does not occur. Even if the ovary is left, but the corpora lutea are destroyed by a galvanic needle, the fixation fails to take place. It is probable that the corpus luteum is a gland, as its structure suggests, and the substance produced influences the wall of

the uterus in such a way that it responds to the presence of the embryo and grows up around it.

It has been shown in the vertebrates that the development of the secondary sexual organs is intimately connected with the presence of the testes. In the insects it appears that this connection does not exist. Oudemanns has shown for Ocneria dispar that when the testes are removed from the male caterpillar, the secondary sexual characters of the male are unaffected. Kellogg has confirmed this result for the silkworm moth. Oudemanns also removed the ovaries from the female caterpillar and found that the female moth showed the normal markings.

Pictet points out that in a few cases there exist a male form and a female form of caterpillar, although as a rule in most animals the secondary sexual differences do not appear until the adult stage. Often the size of the caterpillar is the only external difference that is noticeable between the sexes, the males being smaller than the females. In the case of Orgya antiqua and Orgya gonostigma, however, the female caterpillars are superbly colored, and covered with spines of different shades; the male caterpillars are not only smaller, but simpler and without the spines. In Ocneria dispar the larval sexual dimorphism is marked, but only in the fully formed stage of the caterpillar. Pictet found that when caterpillars of this species are fed on esparcette and dandelion, that furnish ample nutrition, the larvæ develop with great rapidity, and all acquire the characters of the female caterpillar. With pimprenelle, which also gives an abundant nourishment, but not so well as the preceding, the caterpillars that showed the female type of marking were in excess. On the other hand, when fed on walnut leaves, giving insufficient nourishment, the caterpillars all assumed the characters of the male. In the case of other plants that gave insufficient nourishment this effect could not be seen, because the food introduced other effects that changed the aspect of the caterpillar.

The caterpillars of Ocneria dispar normally transform into chrysalids after the fifth moult. The males reach the stage first and the females may still be in the fourth period when the males

have transformed. At this time the females resemble the males, and the secondary sexual differences come afterward, while the females are getting still more food. This difference in the amount of food may be the indirect cause of the secondary sexual differences in these species.

In the crustaceans, Giard has found that when Stenorhynchus is attacked by a parasitic copepod, Sacculina fraissei, the reproductive organs are almost completely destroyed. When this occurs in the male the female characters appear — the smaller claws and broader tail. In the female there is a reduction of the abdominal feet, a condition characteristic of the male. If these effects are directly due to the removal of the sexual organs, as experiment might show, and not due to the effects produced by the parasite, whose roots penetrate to all parts of the body, then they differ from the cases in the insects and are like those of the vertebrates. As yet it is not possible to decide which is the true view until castration has been artificially induced.

We have now passed in review the principal facts connected with the occurrence and development of the secondary sexual characters. We have seen that in the vertebrates their development is connected with the presence of the testes, but that this is not true for the insects so far examined. This difference may be interpreted to mean that in the vertebrates, the stimulus for the development of these characters in the male comes from the reproductive organs. The ability to develop these parts must, nevertheless, be supposed to be latent in the body cells. In the insects the body does not require the stimulus of the reproductive organs to develop the characters of the male. This distinction raises the question as to whether the secondary sexual characters of the vertebrates belong to the same class as the differences observed in insects, and this suggests the further question whether if they are different they may not owe their origin to different factors of evolution.

LITERATURE, CHAPTER XXVIII

(See Chapter XXIX.)

CHAPTER XXIX

SECONDARY SEXUAL CHARACTERS (*continued*)

Theories of the Origin of Secondary Sexual Characters

When Darwin proposed his theory of natural selection in 1859 he brought forward also at the same time his theory of sexual selection to account for the origin of secondary sexual characters. "This form of selection depends not on a struggle for existence in relation to other organic beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring." Darwin believed that the secondary sexual characters have arisen in either of two ways: either as a result of a contest between the males that has led to the development of such structures as the horns of the stag and the spur of the cock; or as the result of selection by the females of the most adorned, or brilliantly colored, or highly scented male individuals. This latter form of selection has brought about the development of such characters as the color, the ornaments, the song, and the scent glands of the males.

Of these two forms of sexual selection the first is merely an extension of the principle of natural selection applied to the male individuals of the same species; while the second form of selection depends on the æsthetic taste of the females.

In 1871 Darwin developed his theory of sexual selection much more fully in his book on "The Descent of Man." Here he appears at times to give the theory precedence over the theory of natural selection itself, and attempts even to account for the development of color and ornamentation, when it exists in both sexes, by assuming that through the selection of the female it

was first developed in the male and was then transferred to the individuals of the other sex.

There are serious objections to the theory of sexual selection, some of which Darwin himself has considered. He points out, for instance, that his theory demands "powers of discrimination and taste on the part of the females which will at first appear extremely improbable." The few instances that Darwin gives to show that such discrimination may really exist are far from convincing. Amongst domesticated animals there is very little evidence that can be brought forward to support this view, and much that is opposed to it. It must be borne in mind that even although the female may be excited by the presence of the male or by his antics and demonstrations, it is essential that she consistently select the most adorned in order that any result may follow. Tegetmeier observed that a game cock, disfigured by being dubbed and with hackles trimmed, was accepted by the females.

Mayer has recently carried out some experiments with the moth Callosamia promethia that show very clearly that the adornment of the male or of the female is not a factor in the selection by the other sex Five females were placed in an open-mouthed glass jar covered by netting. Five males, liberated one hundred feet away, flew to the jar. If the jar was inverted so that its opening was closed, the males did not approach, although the females could be seen through the glass. It appears, therefore, that the males find the female by the sense of smell, not by sight.

Some females were inclosed in a box with an open chimney. The males flew to the chimney, although the females were not visible. When the abdomen of the females were cut off the males flew to these, and paid no attention to the winged body. Wherever a female has stood for some time, the males are attracted to that spot. If the antennæ of a male are cut off, he does not go to the female. These experiments also show that the male finds the female by a sense of smell, and not by vision, although the female is highly ornamented.

Mayer also made some experiments to test whether the females show a choice in selecting the males. The male is dark or blackish; the female reddish brown. The wings of a female were cut off and glued on to the wings of a male, so that he appeared like a female; nevertheless he was accepted by a female, no aversion was manifested, and the mating was normal. The converse experiment was also made. The wings of a female were cut off near the base and the wings of a male were glued on in their place. Such females looked like males, yet the males mated with them as with normal individuals. Clearly, then, neither the coloration of the male nor of the female can be supposed to have a selective value.

Males pay no attention to males with female wings; but will pair readily with a female both of whose wings have been cut off. Even when the wings of both the male and the female have been removed, pairing occurs if they are brought together.

One series of experiments of this kind is not perhaps conclusive, and there is great need for more experimental work along these lines.

There are many other serious objections to be urged against Darwin's theory. I shall give here only a few of the more important ones.[1]

In most groups of unisexual animals — and it is only such that come under the theory — the number of males and females is approximately equal. Therefore even if we admit that the most ornamented individuals are first selected, the remainder of the females must pair with the less ornamented males. In consequence nothing would be gained in successive generations.

It is assumed that by the selection of individual or fluctuating differences the character of the males can be greatly changed. It may be questioned if this is possible, even if rigorous selection be admitted to occur. It is doubtful if anything more could be accomplished in this way than to maintain the standard at a

[1] In my book on "Evolution and Adaptation" I have discussed this topic more fully.

somewhat higher level, which would be lost as soon as the selection stopped.

The process as imagined by Darwin is highly wasteful, for in order to build up the ornamentation of the males, countless individuals must have been sacrificed, yet the end result is of no advantage to the species.[1] If competition is as keen in nature as Darwin supposes, one would think that natural selection itself would soon have put an end to such a wasteful and useless procedure. There cannot be much doubt that the horns of the stag and brilliant coloration of many male birds must expose them to greater danger, so that natural selection ought, from the Darwinian standpoint, to bring about their disappearance.

There is a considerable number of sexual characters, such as the loud voice of the stag, that Darwin believes have been developed through use. In fact, he appeals not infrequently to Lamarck's theory when the evidence is unfavorable to the selection theory. Since the theory of inheritance of acquired characters has itself been brought into question in recent years, it is doubtful if Darwin's position is strengthened by an appeal to such a principle.

The application of the theory to man shows how involved the argument becomes. Darwin thinks that the beard in man has been developed by women selecting those males that had this outgrowth most developed. The absence of the beard in women is explained as the result of men selecting those women that had less beard until it was eliminated. These two conflicting processes are supposed to go on at the same time, or alternately. The greater energy, size, and pugnacity of men have come from their competition with each other, while the standard of beauty has been maintained for both sexes by men selecting the more beautiful women, who have then transmitted this quality to the male. The deeper voice in man has been developed by its long-continued use by the male "under the excitement of love, rage,

[1] Natural selection also is wasteful, since the waste is unavoidable. If amongst individuals of the same species it leads to the survival of the strongest, this may be an advantage, so that in either case the outcome is different from that of sexual selection depending on female choice.

and jealousy." Human song has also been the result of courtship and rivalry.

The theory demands that the females select the most beautiful males, and this implies either that the taste or appreciation of the female must always improve in advance of the improvement in the secondary sexual characters of the male, or that the female is gifted with this appreciation from the beginning. If the former view is held, one may ask how has her taste been improved; if the latter is held, one may ask how she has come to be so gifted. The theory of sexual selection can give no answer to either alternative, yet cannot justify itself without some such assumptions. Other objections might be urged, but these will suffice, I think, to show how improbable it is that the secondary sexual characters can be accounted for on the principle of female selection.

Wallace, who suggested the theory of natural selection simultaneously with Darwin, has never accepted the theory of female selection, and has attempted to explain the facts in a different way. In his essay on "Tropical Nature," published in 1878, he first developed his view, but has given the subject much fuller treatment in his recent book on "Darwinism." He assumes that there is a tendency for the males of most animals, especially birds and insects, to develop a greater intensity of color, and this "tendency" is ascribed to the greater "vitality" of the male. In the female, especially amongst birds, the development of color is rigorously kept down by natural selection, especially in those species that build open or exposed nests. In such cases the female sitting on the nest would be exposed to the attacks of enemies were she brightly colored. In support of this latter view, Wallace points out, the species in which both sexes are equally colored, the kingfishes, woodpeckers, toucans, parrots, turacos, hangnests, and starlings, make their nests in holes in trees, or in the ground, or build a dome over them. The female is in consequence not exposed on the nest. Conversely, when the male is brilliantly colored and the female plain the nest is open. The color, Wallace states, must have adapted itself to the instinct, and not the instinct to the color, because habits

are more difficult to change than color; but Wallace brings forward no evidence to establish this view.

In other vertebrates this hypothesis will not explain the plainer coloration of the females, as Wallace points out, since they do not incubate their eggs. Secondary sexual differences are known in fishes, lizards, and mammals that appear to be similar to those in birds. Wallace has recourse, therefore, to the theory of natural selection amongst the males which has led to the survival of the stronger males. In polygamous races this leads to the successful males becoming the fathers of the next generation. The stronger animals are those whose colors and other such characters will be more highly developed. In monogamous species, and these are by far the most common, the result of competition amongst the males will not produce any result, since the vanquished males will also find mates. Wallace tries to meet this difficulty by pointing out that the males of many insects emerge before the females, and that the males of migratory birds are the first to arrive at the nesting grounds. The most vigorous males will be the first to pair and leave offspring. This precocity is assumed to be an advantage, but it is obvious that it might be also a disadvantage, and we have no means of weighing the relative merits of the individuals that pair first with those that pair at the height of the breeding season.

Wallace thinks that the greater vigor of the males will lead in itself to the higher coloration of that sex, and furthermore he tries to show that the ornaments are more likely to occur over those parts of the animal where the muscular and nervous development is greatest; but the location of the tail of the peacock, the crest of the herons, and many other characters that might be cited would seem opposed to such an assumption.

Darwin has considered Wallace's view in his "Descent of Man" and has pointed out that while the theory might appear to apply to sexual differences in color and ornamentation, it is not obvious how other secondary sexual characters, such as the vocal organs of birds and the scent glands of mammals, could be thus explained. Wallace has replied to this criticism by assuming

that natural selection has first developed these organs as recognition marks by means of which the individuals find each other, and later the greater vitality of the male causes them to develop more fully in that sex.[1]

Cunningham has attempted to account for secondary sexual characters by means of the theory of the inheritance of acquired characters. His effort is to show how the theory will account for these structures, the theory being assumed to be valid, for to the author it is "obvious that if the removal of the testes can affect the development of tissues in the head, the development of the latter may affect the properties of the testes." Such statements only confuse the issue, which, after all, must rest on the experimental proof as to whether or not the special development of parts of the body does bring about corresponding changes in the germ-cells. There has been no difficulty in showing that the removal of the reproductive organs affects the body; but as yet little or no evidence that is satisfactory has been obtained to show the converse to be true.

Cunningham assumes that the use of the secondary sexual organs often subjects them to special mechanical irritation when other organs of the body are not affected. These mechanical strains and pressures affect the development of the organs, and the results are supposed to be inherited. He asks, why are the secondary sexual characters of the male restricted to the male offspring and those of the female to the female offspring? His answer is that "heredity causes the development of acquired characters for the most part only in that period of life and in that class of individuals in which they were originally acquired." The same idea is more fully expressed in the statement "that the direct effects of regularly recurrent stimulations are sooner or later developed by heredity, but only in association with

[1] Lameere also accepts that part of Darwin's theory of sexual selection that assumes the secondary sexual differences to be due to natural selection between the individuals of one sex; but rejects Darwin's idea that the differences can be accounted for by selection of the males by the females. In these respects he agrees with Wallace.

the physiological conditions under which they were originally produced," etc. Thus the secondary sexual characters acquired by the adult male became inherited only by the males and at the same time of life at which they first appeared in the male. As a purely formal assumption no objection can be made to this kind of hypotheses. Our opinion as to whether it is probable or not must be guided by the experimental evidence that can be brought forward in its support. At present this evidence is lacking.

It seems to me that Wallace's view, that the secondary sexual differences may be due to the greater "vitality" of the male (which has resulted from the natural selection of the stronger males), may be given a much simpler interpretation without necessitating the assumption of any process of selection. When we see the wonderful development in all groups of the animal kingdom of pigmentation, and when we realize that there are inherent differences between the males and females of each species, it is not surprising that differences in color might also appear associated with the male and female condition. So long as these differences do not seriously interfere with the existence of the species, they will perpetuate themselves. Only if carried too far might the species exterminate itself. There is no need of selection to account for their origin. At most "selection" might account for their destruction if they develop beyond a certain point.

This mode of explanation will not, I am aware, appeal to those naturalists of the Darwinian school who attempt to explain all organic conditions as the result of usefulness. They seek to find a *purpose* in every existing condition, and therefore try to find some purpose for the secondary sexual differences between the male and the female. That a great number of the characteristics of organisms have a purpose there can be little question. This purpose is the maintenance of the species; but it is not logical to assume that because a great number of adaptations exist, all characters must therefore be adaptations to something or other, at least in the sense that they have a survival value. The

very argument that secondary sexual characters have arisen by sexual selection implies an injurious process that involves a serious loss to the species of the less ornamented individuals, and therefore a lack of adaptation. Thus in the effort to show the purposefulness of the secondary sexual characters, the injury caused to the species has been overlooked.

If it be granted that neither natural selection nor sexual selection can explain the origin of the secondary sexual characters, there opens a wide field for future thought and study. If variations can occur that ultimately culminate in the gorgeous tail of the peacock, the wonderful colors of the humming birds, the splendid antlers of the stags, and the musical, mathematical, and æsthetic development in man, do we not seem to catch a glimpse of a power of progressive development in organisms that, given a suitable environment, may produce extraordinary results? It is improbable that these highly complex structures have been the result of a single variation, and therefore, if the result of several or many successive variations, these must have gone on building up in the same direction. The power of advancing in one direction, unguided by selection, is one of the least appreciated biological phenomena, and yet may be one of profound significance.

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